Ecological investigations of euphausiids at high latitudes.

By

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Thesis offered for the degree of
Doctor of Philosophy
(Biological Oceanography)
in the University of St. Andrews

January 2007

Declaration

I, Ryan Alexander Saunders hereby certify that this thesis, which is approximately 43,000 words in length, has been written by me, that it is a record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

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I was admitted as a research student in April 2003 and as a candidate for the degree of Ph.D in April 2004; the higher study for which this is a record was carried out in the University of St. Andrews between 2003 and 2007.

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Abstract

1. Euphausiids are an important component of high latitude pelagic ecosystems, but there is a paucity of information on their distribution, abundance and population processes on within-year time scales. This thesis encompasses new research into the euphausiid-ocean component of two important high latitude ecosystems (South Georgia and the Irminger Sea) on sub-annual time scales.

2. A new method for measuring abundance of Antarctic krill (*Euphausia superba)* continuously at South Georgia (Southern Ocean) was devised using upward-looking acoustic devices deployed on moorings. These novel platforms provide a new window of observations onto marine systems not open from conventional research vessels. At South Georgia, the moorings provided data at a high temporal resolution giving completely new insight to the function of the coupled biological-physical marine ecosystem. The use of moorings may aid ecosystem-based management at South Georgia and elsewhere.

3. Analysis of mooring data collected between October 2002 and December 2005 indicated a regular annual cycle in krill density: high in summer and low in winter. Mooring estimates of krill density were not statistically different from estimates derived from standard ship-based surveys in adjacent time periods suggesting that the mooring point estimates had relevance in a wider spatial context (c. 100 x 100 km). The results indicated that because of the sharp peaks in the biomass cycle, the exact timing of repeated ship-based acoustic surveys might be critical. Surveys that differ in their timing by only a few weeks might exhibit quite different estimates of biomass because they fall at different points of the cycle. Additionally, within this intra-annual framework, annual ship-based surveys may be able to detect differences between high and low krill years only if they differ by densities of c. 35 g m^{-2} in summer and c. 20 g m^{-2} in winter.

4. The mechanisms driving intra-annual variability in Antarctic krill density at South Georgia are likely to be complex. Analysis of mooring data revealed a possible association between high krill density and low water temperatures (at 200 m) at South Georgia. There was evidence that seasonal variation in krill density off-shelf was linked to seasonal variation in current velocity: marked increases in velocity at the end of summer coincided with marked decreases in krill density and abrupt changes in water temperature characteristic of the Sub-Antarctic Current Front (SACCF). Oceanographic data indicated that the SACCF might have impinged in proximity to the moorings during the winter season. However, krill densities were low during these periods and analyses suggest that seasonal variations in krill density were not driven by seasonal oscillations in the position of the SACCF. The data are not consistent with a pattern of seasonal growth, production and mortality of a resident krill population at South Georgia, but are consistent with the notion of large influxes of krill in early summer, and of a predator-driven reduction at between mid- and late-summer.

5. The seasonal distribution, abundance and growth of key euphauiids in the Irminger Sea, North Atlantic was quantified using the first net haul data from the region since the 1930s. Results show a high degree of spatial heterogeneity in the seasonal distribution of euphausiid abundance/biomass during 2001-2002. There was evidence to suggest regional variation in growth and population processes of *Meganyctiphanes norvegica* and *Thysanoessa longicaudata*, and this corresponded broadly to distinct physical zones in the Irminger Sea. There were, however, no significant links between growth and temperature and chlorophyll *a* concentration. This was attributed to high spatial and temporal variability in biological and physical sampling. These data are a prerequisite for understanding ecosystems dynamics in the North Atlantic, and are important for robust ecosystem-based management strategies.

6. Controls on euphausiid spatial heterogeneity at high latitudes are likely to be complex. Important factors include horizontal advection, temperature, resource availability and behavioural mechanisms. Short-term (intra-annual), small-scale (basin-scale) data are fundamental to understanding variability in euphausiid abundance and distribution on broader spatial and temporal scales in these ecosystems.

Acknowledgements

First of all, I would like to thank my supervisor, Andrew Brierley, for his endless enthusiasm, guidance and support throughout this studentship, and for providing me with so many opportunities to embark on research in exciting places. I am also grateful to Eugene Murphy at British Antarctic Survey for his support as my CASE supervisor.

I thank my colleagues in Pelagic Ecology Research Group, in particular Kirsty Anderson for many valuable and insightful discussions regarding my research, Ben Heywood for help with computer programming, and Martin Cox for advise with modelling and statistics. I am grateful to Anna Ingvarsdóttir and the Marine Productivity Summer School participants at the University of Aberdeen, especially Scott McRobert and Indy Roberts, for assistance with processing zooplankton samples, and to Jim Hunter and Steve Hay for assistance with net sampling during the Marine Productivity cruises. I am also grateful to the masters, officers and crew of RRS *Discovery* for their assistance at sea. From the mooring aspect of the project, I would like to thank Peter Enderlein, Doug Bone and the masters, officers and crew of RRS *James Clark Ross* for efficient deployment and recovery of the moorings; Mark Brandon and Sarah Jenkins for discussion of CTD data; Keith Reid for providing predator-derived krill length-frequency data for calculating krill target strengths; and logistic personnel at British Antarctic Survey for their efforts in recovering a mooring that was dragged prematurely from the seabed by a fishing vessel.

On a personal level, I extend my greatest thanks to Rian Davies, Mireille Consalvey, Jane Freel, Ben Heywood, Jon Good, Anna Morton and Rene Swift for their friendship and support, and for making my time in St. Andrews so enjoyable. Special thanks also go to Louise Langeby for keeping my spirits high during the final stages of this studentship. Finally, I thank my cycle touring team, Dan Cottam and Dave Mapson for their friendship and encouragement.

To Mum, Dad and Miranda
for always being there.

Contents

1. Variability in euphausiid abundance and distribution in high latitude ecosystems: a general introduction

1.1. Introduction

The pelagic ('open sea') environment is that of the water column, from the surface to the greatest depths (Lalli and Parsons 1997). The pelagic environment supports two basic types of marine organism. One type comprises the plankton, or those organisms that are unable to counteract the influence of currents and drift passively in the horizontal plane. Planktonic organisms are divided primarily into two broad functional groups: phytoplankton (autotrophic algae) and zooplankton (heterotrophic animals). The remaining inhabitants of the pelagic environment form the nekton, which are free-swimming metazoans that are strong enough to swim against currents and are therefore independent of water movement (e.g. fish, squid and marine mammals). Marine zooplankton are both taxonomically and structurally diverse, and they function at many levels in pelagic food webs, as consumers, producers and prey (Lalli and Parsons 1997). Ranging in size from microns (protoplankton) to centimeters and meters (metazooplankton), marine zooplankton are also major contributors to elemental cycling and vertical flux (Angel 1997). Thus zooplankton are key components of marine ecosystems.

The open ocean is not homogenous, and interactions between physical (e.g. temperature, salinity, turbidity) and biological (e.g. production) processes result in variability over a range of temporal and spatial scales: the resulting patchiness is a key feature of pelagic ecosystems (Haury et al. 1978). Spatial heterogeneity, in both vertical and horizontal dimensions, has profound implications for ecosystem function and presents problems for sampling zooplankton and hence understanding their distribution of abundance, population processes, and trophic interactions (Pinel-Alloul 1995). A central aim of biological oceanography is therefore to quantify the distribution of zooplankton abundance at a range of spatial and temporal scales, and to identify the major processes that control spatial heterogeneity of zooplankton within

pelagic ecosystems (Lalli and Parsons 1997). This information is vital for understanding and predicting changes in commercially exploited pelagic ecosystems that result from natural and anthropogenic environmental changes, and for effective management of marine resources (GLOBEC, 1997).

Pelagic environments in both polar/sub-polar regions sustain, or have until recently, large stocks of conspicuous animal life (for example, birds, seals, whales and fish) (Smetacek and Nicol 2005). Consequently, these regions have been subjected to commercial exploitation and have been highly disturbed by fishing activity (Clarke and Harris 2003). High latitude ecosystems are also sensitive to shifts in climate on temporal scales ranging from inter-annual (e.g. El Niño/Southern Oscillation) through decadal (e.g. Arctic Oscillation, North Atlantic Oscillation) to long-term secular trends (Clarke and Harris 2003). The effects of global climate change are likely to have profound influences on these ecosystems, as small increases in temperature can lead to large impacts on biotic life-cycles, sea-ice habitats, trophic interactions and possibly ocean circulation (Smetacek and Nicol 2005). In both the North Atlantic and the South Atlantic, the capacity of high latitude marine ecosystems to withstand the cumulative impact of climate change and over-exploitation is of great concern (Clarke and Harris 2003). However, our understanding of ecological processes within high latitude ecosystems is limited and the potential impacts of such global and local pressures are unclear. This is primarily due to limited data. There is a fundamental need for data on both the distribution of zooplankton abundance and biological-physical interactions of key zooplankton groups in these ecologically important ecosystems. The present study therefore encompasses novel research into spatial and temporal variability of key zooplankton within high latitude ecosystems. Specifically, this thesis focuses on euphausiids at South Georgia (South Atlantic) and in the Irminger Sea (North Atlantic). By studying the ecology of euphausiids in these two regions, the thesis aims to provide some insight into the most important biological and physical processes that control spatial/temporal heterogeneity in zooplankton abundance and distribution at high latitudes. In this chapter, I provide some background information on high latitude ecosystems and review the relevant scientific literature on the ecology of key euphausiids within the South Georgia and Irminger Sea ecosystems.

1.2. General features of high latitude ecosystems

The Scotia Sea (southwestern Atlantic sector of the Southern Ocean; 54ºS) and the Irminger Sea (eastern North Atlantic; 64 ºN) are situated in sub-polar regions and are both examples of high latitude marine ecosystems (Longhurst 1998). In many respects South Georgia and the Irminger Sea are very different systems (Figure 1.1). South Georgia is a narrow, mountainous island with a broad continental shelf, lying within the open ocean in the Atlantic sector of the Southern Ocean (Figure 1.2; Atkinson et al. 2001).

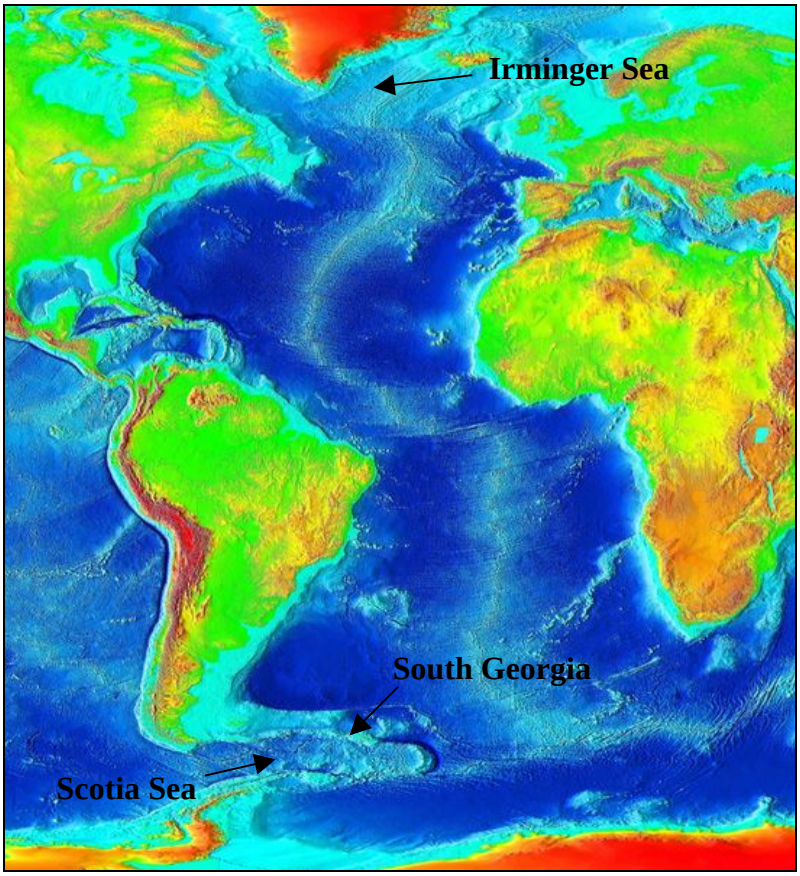

Figure 1.1. Map of the Atlantic Ocean (http://en.wikipedia.org/wiki/Atlantic_Ocean).

In contrast, the Irminger Sea is situated in a relatively deep-water basin, bounded to the west and the north by the continental shelves of Greenland and Iceland, and to the east by the Mid-Atlantic Ridge (Figure 1.4). These systems are also very different in terms of underlying oceanography (see below). However, both regions have some general unifying features. High latitude pelagic environments are characterised by low

water temperatures (usually <5 ºC; Lalli and Parsons, 1997), pronounced seasonal oscillations in incident solar radiation, and are influenced to some extent by waters of polar origin and by the presence of seasonal sea-ice in the polar sectors (Smetacek and Nicol 2005). High latitude ecosystems are also generally characterised by a single peak of primary production during short seasonal windows when light is available (late-spring/summer) (Holliday et al. 2006; Longhurst et al. 1995), the timing and extent of which has a large influence on ecosystem structure (Falk-Petersen et al. 2000). Despite low temperatures and strong seasonality in light, high productivity levels are found in high latitude regions, and the productivities of polar/sub-polar ecosystems are similar to those of lower latitudes during the summer season (>5 g C m^{-2}) (Longhurst et al. 1995; Smetacek and Nicol 2005). However, meteorological and hydrographical forcing factors (e.g. light and nutrient availability) are more variable at high latitudes than at low latitudes, and as a consequence, primary production in these systems is highly variably, not only between seasons, but also over periods of years to decades (Sakshaug 1997). Pelagic animals within high latitude ecosystems are therefore exposed to highly variable food supply (Falk-Petersen et al. 2000).

Temperature, food availability and sea-ice have a pronounced impact on the life-cycles and distribution of marine zooplankton, and many groups have developed a wide range of physiological and behavioural adaptations that enable them to survive under often-harsh conditions (Clarke and Harris 2003; Huntley and Niiler 1995). For example, many herbivorous zooplankton species, including euphausiids and copepods, biosynthesize and store high-energy lipid reserves that enable the animals to survive periods of low food availability and permit them to reproduce at appropriate times of year (Falk-Petersen et al. 2000). Due to the cold water temperatures and variable food availability, high latitude zooplankton often exhibit variable recruitment success, slow metabolic and growth rates, relatively long life cycles, and a large body size compared with congeners from warmer, low latitudes seas (Longhurst 1998). The presence of sea-ice has a vital role in high latitude ecosystem function as it provides a habitat for many zooplankton species, and the life-cycles of many groups are tightly coupled with seasonal sea-ice dynamics (Huntley and Niiler 1995). For example, the dense growth of sea-ice organisms (e.g. algae) on the periphery of ice floes provides an important food source for many zooplankton groups during the winter when food in the water column is not present (Scott et al.

1999). Also, some pelagic organisms, such as the Antarctic krill, utilises the sea-ice as a refuge from predation (Marschall 1988; Quetin and Ross 2001; Siegel and Leob 1995). In the Irminger Sea, sea-ice is present around the East Greenland shelf and may have direct influence on pelagic organisms in the region (Einarsson 1945). Polar sea-ice does not extend as far as South Georgia, however, the South Georgia ecosystem is still impacted by sea-ice as the island lies in the path of water masses of polar origin that contain zooplankton populations from the sea-ice sectors further south (Einarsson 1945; Murphy et al. 1998).

As well as similarities in many environmental characteristics, such as low water temperature, extreme photoperiod and the influence of sea-ice, the South Georgia and Irminger Sea ecosystems are further unified by the spatial scale at which oceanographic processes exert control over zooplankton populations. Huntley and Niiler (1995) assert that horizontal advection is the single most important mechanism by which physics of high latitude seas exerts control on zooplankton distribution/population dynamics, and that the physical processes in high latitude seas are different from those in all other oceans. For example, advection determines whether or not zooplankton (and to some extent, nekton) will reside in food-rich (e.g. shelf-break regions) or food-poor regions (e.g. Antarctic Circumpolar current), and the morphology of the advective features further determines the residence time in a given food regime. Thus advection has a direct impact on rates of growth, mortality, reproduction, and ultimately, the distribution of zooplankton abundance (Huntley and Niiler 1995). Advective processes (e.g. baroclinic eddies and frontal zones) at high latitudes are different to those at lower latitudes primarily due to differences in their natural horizontal scales. The spatial scale of circulation (determined by the internal Rossby radius) is dramatically altered with latitude, and advective forces at high latitudes operate at much smaller scales (order 10 km) to those at lower latitudes (order >100 km in the subtropics) (Huntley and Niiler 1995). Consequently, the intensity of advection on such small scales causes zooplankton populations to be more highly dispersed in high latitude systems, and this high spatial heterogeneity has important implications for understanding ecosystem function in these regions. Thus in order to understand, model and ultimately predict the euphausiid-ocean component of pelagic ecosystems at high latitudes with a high degree of certainty, it is important to collect biological and oceanographic data at a high temporal and spatial resolution.

Short-term (intra-annual), basin-scale (5-100 km) data are prerequisite for quantifying and understanding longer-term, broad-scale variation in euphausiid-ocean dynamics in relation to a changing environment. High latitude ecosystems are however remote and experience often adverse weather conditions. Consequently, logistic and financial constraints have restricted the time over which data on pelagic ecosystems in these regions can be obtained from conventional ship-based surveys. These factors have particularly limited at-sea sampling regimes during the winter seasons when weather conditions are poor and data returns are low.

1.3. High latitude food webs and ecosystem function

The classic view of high latitude food chains is that they are shorter (i.e. fewer trophic levels) and more simple than those at lower latitudes, and that they are dominated by a few keystone organisms (Lalli and Parsons 1997). This notion stems largely from the early *Discovery* investigations in the Southern Ocean which concluded that polar ecosystems channel a greater proportion of primary production to warm-blooded predators than those at lower latitudes (Hart 1934; Hart 1942). Furthermore, it is commonly assumed that species- and trophic-diversity are related (Ulanowicz 2000). Although many zooplankton groups are successful in high latitude regions, recent studies have shown that zooplankton communities in the oligotrophic tropical regions typically contain more species than their polar/sub-polar counterparts, and that the distribution of many zooplankton taxa exhibits a latitudinal cline (Angel 1997; Woodd-Walker et al. 2002). Thus it has been implied further that pelagic food chains at high latitudes are simpler and shorter than those at low latitudes as there are fewer links (Lalli and Parsons 1997). However, research conducted over the past two decades has shown that the concept of short, low-diversity high latitude food chains is over simplistic, and that high latitude pelagic food webs are not shorter or simpler than elsewhere (Smetacek and Nicol 2005). Although comparatively few zooplankton groups comprise the bulk of food for marine predators, the planktonic base of their food supply is equivalent in phylogenetic diversity to that in low latitude regions, implying that the structure and functioning of pelagic food webs are broadly similar across all latitudes (Smetacek et al. 2004; Smetacek and Nicol 2005). Microbial interactions and biogeochemical fluxes are also as complex in high latitude

ecosystems as they are at lower latitudes (Smetacek et al. 2004). Our understanding of the complex trophic interactions and energy budgets within high latitude pelagic food webs is limited, as is our understanding of the bio-regulatory controls on high latitude ecosystem structure (Lalli and Parsons 1997).

At the simplest level, there are two contrasting hypotheses for ecosystem control on zooplankton (Gliwicz 2002):

- Bottom-up processes: the supply of nutrients by physical forcing and their conversion to organic matter by photosynthesis exert control over zooplankton populations and thus high trophic levels (i.e. fish and other predators) (Clark et al. 2001).
- Top-down processes: carnivores may exert control over ecosystems through predation on zooplankton, causing a trophic cascade whereby the phytoplankton population benefits from a reduction in grazing pressure (Verity and Smetacek 1996).

It is widely assumed that most marine ecosystems are controlled by bottom-up processes (Clark et al. 2001). However, there is no simple relationship between the magnitude of primary production and the biomass and composition of higher trophic levels (Smetacek and Nicol 2005). The complexity of high latitude ecosystem interactions is demonstrated by the marked long-term (decadal-scale) fluctuations in upper-level predator populations that are characteristic of all high latitude systems, which seem to be associated with corresponding changes in local oceanography and climate (Smetacek and Nicol 2005). Furthermore, it has been demonstrated that predation or top-down trophic effects could be equally important in ecosystem control by specifying the occurrence of certain taxa and the biomass within adjacent trophic levels (Verity and Smetacek 1996). These authors suggest that key species, because of unique combinations of life-cycle properties, physiological processes and metabolic demands, may exert a dominant role in the extent to which predatory interactions cascade through pelagic food webs at high latitudes. As human-mediated change has influenced high latitude ecosystems in both hemispheres, and is likely to continue to do so, unravelling the effects of bottom-up and top-down forcing on these potentially sensitive pelagic systems is an immediate task facing biological oceanographers (Clarke and Harris 2003; Smetacek and Nicol 2005). Thus there is an increasing need

for information on all food web components to identify possible trophic cascades and forecast future climate scenarios in these regions (Pauly et al. 2002).

1.4. Importance of euphausiids at high latitudes

A key zooplankton group in high latitude pelagic ecosystems are euphausiids (*Euphausiacea*). Euphausiids are holoplanktonic crustaceans and there are 85 recognised euphausiid species. The group is widespread throughout the world's oceans, but the greatest euphausiid species diversity, numerical abundance and standing stocks of euphausiid biomass are found at mid- to high latitudes (Boltovskoy et al. 1999; Mauchline and Fisher 1969; Nicol and Endo 1999). Compared to other zooplankton, high latitude euphausiids are relatively large (up to 60 mm) and they frequently dominate (in terms of biomass) zooplankton communities, particularly over the continental shelf and in regions of high environmental productivity. Many high latitude euphausiid species display pronounced diurnal vertical migration (DVM) and traverse distances in excess of 200 m at night (Mauchline 1980a). To a large extent euphausiids are viewed as passive drifters in the flow field (Hofmann and Murphy 2004). However, studies have shown that many high latitude euphausiids (especially Antarctic krill, *Euphausia superba*) form dense swarms or aggregations that are capable of active horizontal movement (Hamner 1984; Hamner and Hamner 2000; Mauchline 1980a; Siegel 1988; Sprong and Schalk 1992), and that these animals are able to modulate their horizontal position in the water column via vertical migration (DVM) through different motile water masses (though the external cues mediating such behaviour are unclear) (Tarling et al. 1998). Thus euphausiids are not strictly planktic and it is often important to view euphausiids as being nektic (Nicol 2003).

Due to their large body size, often-high abundance and omnivorous diet, euphausiids play a vital role in pelagic ecosystem function at high latitudes and are of growing importance to human exploitation (Siegel 2000a). High latitude euphausiids consume phytoplankton and are capable of transferring surface production to the sediments directly (via DVM). These organisms therefore have a significant function in carbon flux (Noji 1991). High latitude euphausiids are also thought to exert considerable predatory impact on mesozooplankton populations (Atkinson et al. 1999; Atkinson et

al. 2001; Bamstedt and Karlson 1998), whilst forming a central component of the diet of a number of predators, including whales, various avian species and fish species (Croxall et al. 1999; Gonzalez et al. 2000; Macauley et al. 1995; Vikingsson 1997). Thus euphausiids act as important conduits through which primary production is channelled to upper-trophic-level species, such as commercially targeted fish, and provide the bulk of food to many warm-blooded marine predators. Furthermore, high latitude euphausiids are considered to be significant predators of fish larvae, and may have a direct impact on the magnitude of pelagic fish recruitment in some regions (Paradis et al. 1996; Theilacker et al. 1993).

1.5. Euphausiids in the Southern Ocean and at South Georgia

1.5.1. General distribution and abundance of Antarctic krill

The following species of euphausiid occur in the Southern Ocean: *Euphausia superba*, *E. crystallorophias*, *E. vallentini*, *E. triacantha*, *E. frigida*, *Thysanoessa vicina* and *T. macrura* (Gibbons 1997). Antarctic krill, *E. superba*, is the most dominant euphausiid species in the Southern Ocean, both numerically and in terms of biomass (Atkinson et al. 2001). Consequently, the species has been widely studied (see reviews by Siegel, 2005 and Nicol 2006). There are, however, still considerable uncertainties about key elements of its biology and of the forces that determine its distribution and abundance (Murphy et al. 2004a).

In general, Antarctic krill is a long-lived (5-7 years, reaching sexual maturity after 2 years), schooling species (reaching densities of up to 10,000-30,000 ind. m^3; Hamner and Hamner, 2000) with high metabolic demands that are met through a varied diet, and with a complex life cycle that utilizes, in different phases, pelagic, benthic and sea-ice environments (see review by Nicol 2006). The species also displays pronounced ontogenetic migration (Marr 1962). Antarctic krill has a circumpolar distribution with the main centres of concentration around the island groups and along the continental shelf –break and slope with high summer chlorophyll concentrations (Atkinson et al. 2004; Everson 2000). The Antarctic Polar Frontal Zone- that is the circumpolar front where the cold Antarctic surface water submerges below the

warmer sub-Antarctic waters- generally defines the northern limit of its distribution (approximately 55º S) (Everson 2000). Thus krill at South Georgia are at the limit of their distributional range. Although the distribution pattern of krill is relatively well established, its overall biomass around Antarctica remain uncertain (Atkinson et al. 2004; Everson 2000). Calculations based on potential consumption of primary production by krill suggest a maximum of 4.4 billion tonnes, and estimates of predator consumption suggest a krill requirement of for 150-300 million tonnes (Priddle et al. 1998). Estimates of krill abundance from acoustic surveys indicate a biomass of between 60 and 155 million tonnes, whereas scientific net surveys suggest estimates that are an order of magnitude lower (Nicol et al. 2000). Regionally, the South Atlantic has been confirmed as the area where the largest krill concentrations and the highest densities are located (Atkinson et al. 2004), though the conditions that allow this high abundance are not well defined (Constable et al. 2003). Analysis of all available scientific net data have indicated a potential 80% decline in krill in this region between 1974 and 2004 (Atkinson et al. 2004). However, the trend is difficult to verify as data from acoustic surveys exhibits different trends from those determined from net-based surveys (Hewitt et al. 2003). The suggestion of negative trends in krill abundance and distribution is still cause for concern and requires further investigation (Smetacek and Nicol 2005).

1.5.2. The trophic role of Antarctic krill

Antarctic marine ecosystems are largely dependent on Antarctic krill as it is a major macro-herbivore and the key prey item for a number of higher-predators including whales (*Balaenoptera acutorostrata*), seals (*Arctocephalus gazelle* and *Lobodon carcinophagus*) commercially targeted fish (*Champsocephalus gunnerii*), birds (*Pygoscelis paupa*) and squid (*Martialia hyadesi*) (Everson 2000). Most species in the Antarctic are only one or two trophic levels away from krill (Figure 1.2). Antarctic krill are also fished commercially in the Southern Ocean, and the Southern Ocean krill fishery has prospects for becoming the largest global fishery (Nicol and Endo 1999). Effective resource management of the species is therefore vital, but this is complicated by the inter-annual variation in its abundance throughout its distributional range (Everson 1992b).

The data on the abundance of krill comes from research surveys at South Georgia using a combination of acoustic methods and net sampling. During the last few decades these surveys have shown that there have been summer seasons (1977/78, 1983/84, 1990/91, 1993/94, 1998/99) when krill biomass has been much reduced in the South Georgia area, typically being only ~5 to 10% of the long term mean (Brierley et al. 1999b; Fedoulov et al. 1996; Murphy et al. 1998). Other indirect information on the variability of krill in the region is also available. This includes data from the krill fishery (Fedoulov et al. 1996), analyses of diet and condition of commercial fish species (Everson et al. 1997; Kock et al. 1994) and from studies on avian and mammalian population and behavioural dynamics (Croxall et al. 1988; Croxall et al. 1999).

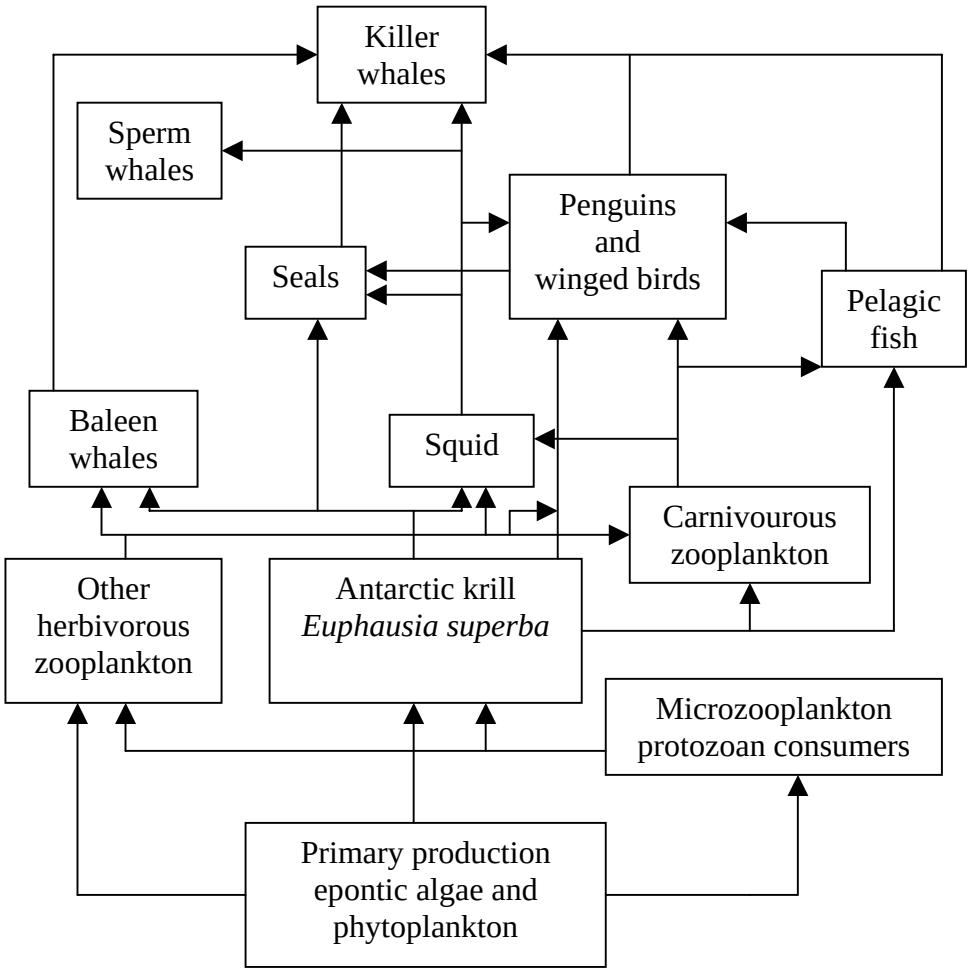

Figure 1.2. A simplified representation of the Southern Ocean food web as presented in Lalli and Parsons (1997).

These data are consistent with the biomass surveys, and such studies have highlighted the possible impact of krill fluctuations on the ecosystem. In years when krill abundance is low, the survival and breeding success of avian and mammalian krill predator species, such as gentoo penguins (*Pygoscelis paupa*) and Antarctic fur seals (*Arctocephalus gazella*), is dramatically reduced (Croxall et al. 1999). Icefish condition and possibly their survival and breeding success also appear to be impaired in 'poor' krill years (Everson et al. 1997; Kock et al. 1994). Another possible effect of fluctuating krill abundance in the area is that alterations in the plankton dynamics and potentially biogeochemical cycling may occur, significantly influencing processes at lower trophic levels (Atkinson et al. 2001; Priddle et al. 1997).

1.5.3. Potential mechanisms generating variability in Antarctic krill populations

Although variability in krill abundance has been well documented, the causative factors remain unclear. A number of explanations for the variability in krill abundance at South Georgia have been suggested, and population processes, ocean currents and sea-ice have been highlight as important factors.

Population dynamics and demographic processes

Krill at South Georgia are not thought to comprise a self-sustaining population (Mackintosh 1972; Marr 1962), and immigration and recruitment success are key factors in the demography of populations that are not reproductively self-sustaining (Reid et al. 1999b). A direct or indirect physical effect on these processes could significantly alter the population structure, thereby causing a reduction in krill availability in a particular area (Murphy et al. 1998). Fluctuations of certain year/size classes in the length-frequency distribution of krill at South Georgia have been well documented (Mackintosh 1972; Reid and Arnould 1996). It has been suggested that the variability in krill abundance at South Georgia could be caused by the failure of a single recruiting year class in the region supplying krill to the island (Murphy et al. 1998; Reid et al. 1999a; Reid et al. 1999b). Murphy et al. (1998) demonstrated the potential effect of such recruitment failure using data from a population model. Reid et al. (1999b) examined weekly samples of krill from the diet of Antarctic fur seals

during the breeding season at South Georgia between 1991-1997 and found a consistent pattern of change in the krill population structure, especially during years of low krill abundance.

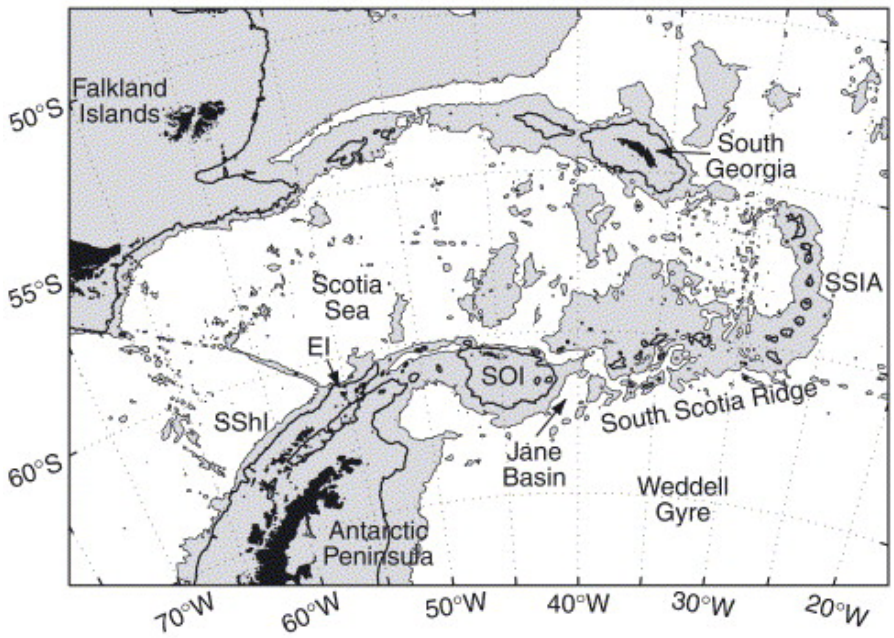

Figure 1.3. Bathymetry of the Scotia Sea region: areas shallower than 3000 m are shaded grey and the 1000 m isobath is shown. Abbreviations are denoted EI- Elephant Island, SShI- South Shetland Islands, SSIA- South Sandwich Islands Arc, SOI- South Orkney Islands. Figure taken from Murphy et al. (2004).

Using these data and putative size/age-group cohorts in the length-frequency distribution, Reid et al. (1999b) suggested that years of low krill abundance were characterised by large mean krill length, indicative of an immigration failure by smaller, juvenile krill the previous year (Reid et al. 1999a). From this, some short-term predicative capability has developed (Reid et al. 1999a). The study also suggested that the timing and magnitude of the incoming year class from the source region might be a crucial factor in determining krill biomass at South Georgia.

The Antarctic Peninsula is a potential source for krill at South Georgia and the region is thought to be pivotal for krill recruitment and in the production of year classes (Siegel and Leob 1995). A key environmental process that can affect krill productivity and recruitment at the source of origin is the distribution and abundance of sea-ice (Murphy et al. 1998; Siegel and Leob 1995). The extent of sea ice cover in the

Southern Ocean has been shown to oscillate regionally with a 4 to 5 year periodicity as the Antarctic Circumpolar Wave rotates around the continent (Murphy et al. 1995; White and Peterson 1995). Recruitment of juvenile krill in the Antarctic Peninsula region has been linked to the extent and duration of ice in the previous season (Quetin and Ross 2001), the environment beneath winter sea-ice apparently providing favourable conditions for the development of krill larval stages (Daly 1990). If krill at South Georgia originate from the Peninsula region, then seasons characterised by increased sea-ice cover in the sector could propagate high krill abundance to the island and other downstream locations (Siegel and Leob 1995). Kawaguchi & Satake (1994) observed large numbers of krill in the vicinity of the South Shetland Islands following a season of extended ice cover, and Brierley et al. (1999a) showed that krill abundance at South Georgia varied in phase and without lag with variation at the Antarctic Peninsula. Reid et al. (1999b) observed almost simultaneous recruitment failures in krill populations at South Georgia and at the Antarctic Peninsula. Also, recent modelling studies suggest that krill populations at South Georgia are similar in size structure to those at the South Shetland Islands once regional differences in growth and mortality are accounted for, further indicating large-scale linkages across the Scotia Sea (Murphy and Reid 2001; Reid et al. 2002).

The variability in krill abundance observed at South Georgia cannot, however, be entirely attributed to krill variability at the Antarctic Peninsula. Murphy et al. (1998) reported that some year classes that were considered strong in the Peninsula region were completely absent from the South Georgia area, raising the possibility of additional sources of variability operating in the South Georgia/Scotia Sea ecosystem. Other studies that have been conducted to examine potential links between the two sites have been inconclusive, mainly due to confusion over the timing of spawning pulses and age determination of individuals (Leob et al. 1997; Siegel 2005; Siegel and Leob 1995). Further discrepancy lies in the fact that the amplitude of change at the two locations differs considerably, again, suggesting that there are additional factors affecting the abundance of krill at South Georgia other than a simple “conveyor-belt” transport mechanism carrying krill from the Peninsula region to the island (Brierley et al. 1999a). Additional periodic recruitment from other sources, such as the Weddell Sea, could explain the observed amplitude discrepancy (Watkins et al. 1999b). If so, it is possible that a separate suite of factors, originating in a different area of

Antarctica and affecting a separate population of krill, may also influence the pattern of variability at South Georgia. The complex nature of krill flux in the Southern Ocean makes understanding population changes at South Georgia difficult. However, investigations to elucidate recruitment indices in the Weddell Sea together with DNA-based genetic studies of krill populations around Antarctica are currently being undertaken to determine the origins of krill populations at South Georgia (British Antarctic Survey Core Science Programme *Discovery 2010*).

Large-scale transport mechanisms

Ocean currents, coupled with active vertical and horizontal migrations by krill populations, have a strong impact on the distribution of abundance of Antarctic krill in the Scotia Sea and are important in determining krill availability at South Georgia (Hofmann and Murphy 2004; Murphy et al. 2004a; Nicol 2006; Thorpe et al. 2004). However, the systems of ocean currents around Antarctica and throughout the Southern Ocean are not simple. The Southern Ocean is dominated by the eastward flow of the Antarctic Circumpolar Current (ACC) that is a band of large zonal transport that circulates uninhibited around Antarctica. It is steered by regional bathymetry; in the Scotia Sea, the South Scotia Ridge deflects the southern part of the ACC northwards towards South Georgia (Thorpe et al., 2002; Figure 1.3). Within the ACC are cores of higher velocity current associated with thermohaline fronts (Nowlin and Klinck 1986). The southern ACC front (SACCF) has been identified as one of three major fronts in the ACC by Orsi et al.(1995). It has been suggested that the SACCF has a crucial role in krill transport to South Georgia since it passes close to Antarctic Peninsula and the Southern shelf of South Georgia before retroflecting around the northern shelf of the island (Hofmann and Murphy 2004; Murphy et al. 2004a; Orsi et al. 1995; Thorpe et al. 2002).

In a study focussed on the frontal flows, Hofmann et al. (1998) noted that the rates of transport in the SACCF were potentially high and that krill transit times across the Scotia Sea can be as rapid as 140-160 days. Data from a physiological growth model, however, demonstrated that food resources across the Scotia Sea were not sufficient to sustain krill growth and survival during such rapid transport (Fach et al. 2002). Fach et al. (2002) suggested an alternative transport scenario, whereby krill originating

from the Peninsula overwinter under the sea-ice that extends northward from the Weddell Sea into the Scotia Sea before being transported to South Georgia the following year. Such interrupted transport would allow krill to over winter in a potentially better feeding environment, and facilitate growth to a size that is similar to that observed within populations at South Georgia (Fach et al. 2002). Furthermore, the model of Hofmann et al. (1998) assumed the location of the SACCF to be fixed. In reality, the region is oceanographically very dynamic, with intense mesoscale eddy and frontal variability (Brandon et al. 2000). Indeed, Thorpe (2001) demonstrated that the proximity of the SACCF relative to South Georgia could change seasonally. Such variability in oceanic circulation systems may have a direct effect on the distribution and transport pathways of krill in the Scotia Sea, resulting in a variable krill flux into the South Georgia area (Murphy et al. 1998; Thorpe et al. 2002). It has been hypothesised that the abundance of krill at South Georgia may increase at times when the SACCF impinges more closely, bringing cooler, krill rich waters into the vicinity (Thorpe et al. 2002). Recent studies have recorded a large flux of krill associated with the SACCF north of South Georgia (Murphy et al. 2004b). However, there is currently very little empirical data to substantiate any clear links between fluctuations in krill abundance and variability in ocean transport systems. This is primarily due to limited at-sea sampling.

1.5.4. Intra-annual variability in abundance of Antarctic krill

Although there is much evidence to suggest that krill abundance at South Georgia varies on an annual basis, there is only very limited data on the scale of within-year variability. Information on an intra-annual time scales is important for the implementation of robust ecosystem-based management strategies at South Georgia to minimize the potential overlap between natural krill-predators and the commercial krill fishery (Everson 1992b; Nicol and Endo 1999). Most at-sea data available on the South Georgia pelagic environment arise from relatively brief research cruises (typically 2 weeks) conducted at a single time point per year (usually summer). On the few occasions when more than one research cruise per year has collected measurements at the island, marked intra-annual variation in krill abundance has been detected (Brierley et al. 2002b; Brierley et al. 1999b). This raises the possibility that

apparent inter-annual variability is actually a temporal alias of shorter-term, intra-annual variability and this has potentially worrying consequences for analyses of ecosystem processes at South Georgia that are based on short-term cruise observations. Another important aspect of ecosystem management at South Georgia is the elucidation of response functions of krill predators to fluctuating krill abundance at certain life stages or times of the year. Low krill abundance at the peak of the predator breeding season, for example, could have a more detrimental impact on the ecosystem than would a krill scarcity during winter (Croxall et al. 1999). Present at-sea sampling regimes are unable to resolve such responses and it has not yet been possible to link predator breeding performance indices to krill abundance because of the differences in time scales of vessel surveys and the breeding season (however, see Reid et al. 2005; Reid et al. 2004). Also, it has not yet been possible to address in detail the major physical processes driving short-term, intra-annual variability in krill abundance at South Georgia due to limited empirical data. New approaches for obtaining biological and physical time-series data at South Georgia are required, and the use of moored instrument arrays is one promising solution for monitoring krill abundance in relation to underlying physical processes at an appropriate temporal resolution (Brierley et al. 2006; Cochrane et al. 1994; Holliday and Pieper 1995). This investigation aims to develop and substantiate a robust method for monitoring short-term variability in krill abundance at South Georgia using moorings, and to quantify the timing and magnitude of intra-annual variation in krill abundance in relation to underlying physical processes.

1.6. Euphausiids in the eastern North Atlantic and Irminger Sea

1.6.1. General distribution of key euphausiids in the North Atlantic

Several species of euphausiids are found commonly in the eastern North Atlantic (Einarsson 1945; Mauchline 1980a; Saunders et al. 2007). These species include: *Meganyctiphanes norvegica, Thysanoessa longicaudata*, *T. inermis*, *T. raschii*, *Thysanopoda acutifrons*, *Euphausia krohni, Nematoscelis megalops*, *Nematobrachion boopis* and *Stylocheiron maximum*. The Northern krill, *M. norvegica*, and *T. longicaudata* are the most important euphausiid species in the North Atlantic

(Mauchline 1980a). *M. norvegica* attains the largest body size (up to 45 mm) among the euphausiid species of the northern hemisphere. The species occurs within a temperature range of 2-15 ºC (Lindley 1982) and its distribution covers an exceptionally wide geographic range from the east coast of Canada to western Europe, including the Mediterranean and regions of the Artic (Mauchline and Fisher 1969). These diverse habitats and the often-high biomass of *M. norvegica* reflect its ability to physiologically and behaviourally adapt to different oceanographic regimes (Cuzin-Roudy et al. 2004; Tarling et al. 1998). *M. norvegica* is most common over continental slopes, oceanic ridges and deep continental shelf waters, occurring at depths between 100-500 m (Einarsson 1945; Mauchline and Fisher 1969). *T. longicaudata* is a comparatively smaller euphausiid species (up to 16 mm) than *M. norvegica*. The species is the most abundant euphausiid in the oceanic surface waters of the Boreal North Atlantic, but is confined within this region, breeding neither in the Arctic nor sub-tropical waters (Lindley 1977; Lindley 1978). Lindley (1977) noted that the main centre of abundance of the species lies over the deep and cold waters of the Labrador-Irminger Gyre. Marked inter-annual variation in abundance of both these euphausiids has been observed throughout their geographic range (Dalpadado and Skjoldal 1996; Lindley 1977; Siegel 2000a; Ulmestrand and Hagström 1992).

1.6.2. General biology of M. norvegica and T. longicaudata

M. norvegica

The biology of *M. norvegica* has been studied by various authors throughout its distributional range (Astthorsson and Gislason 1997; Boysen and Buchholz 1984; Cuzin-Roudy et al. 2004; Einarsson 1945; Falk-Petersen and Hopkins 1981; Jörgensen and Matthews 1975; Labat and Cuzin-Roudy 1999; Mauchline 1960). These studies indicate that *M. norvegica* populations are adapted to very different environments and trophic conditions along European coasts and adjacent seas, from the shallow, cold (5- 10 ºC) Clyde Sea area (western Scotland), Kattegat (east Denmark), and Skagerrak (west Sweden), to the deep and constantly warm (~13 ºC) and oligotrophic Ligurian Sea (northwest Mediterranean). These adaptations are often manifested as differences in growth and reproductive development (Cuzin-Roudy

2000; Cuzin-Roudy et al. 2004) and possibly differences in DVM strategies (Tarling et al. 1999). For example, the reproductive season of *M. norvegica* is relatively long for temperate boreal regions (spring and summer) and short in the Mediterranean (late winter- early spring), in coincidence with productive season for phytoplankton and zooplankton in these areas (Cuzin-Roudy et al. 2004). This variation in spawning behaviour has led to the suggestion that reproductively isolated populations might exist (Siegel 2000b). It has also been noted that *M. norvegica* in fjordic environments attain larger body sizes and are potentially more productive than individuals of the open ocean, which might be linked to regional differences in temperature and food availability (Cuzin-Roudy et al. 2004). In general, *M. norvegica* reaches sexual maturity after one year in the waters around Scotland, Iceland, Norway and in the Irminger Sea, with individuals surviving for about two years (Einarsson 1945; Falk-Petersen and Hopkins 1981; Mauchline 1960; Saunders et al. 2007). The species has a long and broadly defined spawning period in these waters, from the end of March to the end of July. However, population dynamical studies in the Clyde Sea and Kattegat have shown that *M. norvegica* may produce two or three broods per year (Boysen and Buchholz 1984; Mauchline 1960). Cuzin-Roudy & Buchholz (1999) also noted that spawning periods may vary inter-annually in length and timing, the onset and completion of the reproductive period changing by approximately ±1 month over the distributional range.

T. longicaudata

The population dynamics of *T. longicaudata* have been described in detail from Continuous Plankton Recorder (CPR) surveys conducted throughout the North Atlantic (Lindley 1977; Lindley 1978), and from net haul data in other regions such as Korsfjorden (western Norway; Jörgensen & Matthews, 1975), northern Iceland (Astthorsson and Gislason 1997), and the Barents Sea (Dalpadado and Skjoldal 1996). In general, it has been concluded that the species has an annual life cycle, with the life span of an individual being from 12 to 16 months. *T. longicaudata* reaches sexual maturity at around 1 year old and produces one generation during a single spawning pulse during late April to late May. The timing of reproduction in the spring season has been correlated with mean-surface temperature for this species (Lindley 1978). As with *M. norvegica*, *T. longicaudata* displays pronounced variability in life cycle

characteristics throughout its distributional range that are possible adaptations to different oceanographic conditions (food availability and temperature). For example, Lindley (1978) observed that the species produces discrete generations during two annual spawning pulses in the warmer waters of the eastern North Atlantic, as opposed to just one in the colder, more western waters. *T. longicaudata* also demonstrates a high degree of plasticity in age structure and maturity development between the boreal and Arctic regions of the Atlantic, with individuals attaining a higher maximum age (+2 years) and size in the Arctic/sub-Arctic (e.g. Barents Sea) than at their southern distributional limits (Astthorsson and Gislason 1997; Dalpadado and Skjoldal 1996). Thus conditions appear more favourable for the survival of *T. longicaudata*, and other species in the genus *Thysanoessa*, in the colder water regions at high latitudes where individuals grow to a larger size and older age (Siegel 2000b).

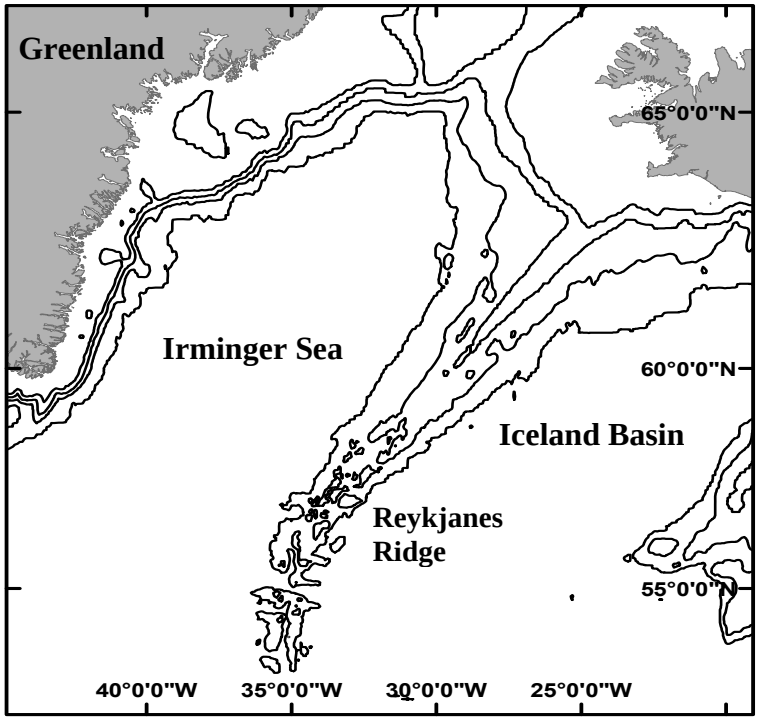

Figure 1.4. Map of the Irminger Basin. The 500 m, 1000 m, 1500 m and 2000 m isobaths are also shown.

Small-scale (within-basin) variation in the Irminger Sea

The North Atlantic aspect of this investigation focuses on the Irminger Sea (Figure 1.4), a region where data on zooplankton abundance and population dynamics are scarce. The Irminger Sea is a very oceanographically dynamic region. Circulation in the surface layers and at depth is counterclockwise around its margin (Lavender et al. 2000). The Irminger Sea can be divided into at least three distinct regions based on the oceanographic properties of the upper 500 m of the water column (Holliday et al. 2006): the Central Irminger basin, which contains an oligotrophic, weakly cyclonic gyre; the region to the west of the crest of the Mid-Atlantic Ridge dominated by the northward flow of the Irminger Current; and the region over the Greenland Shelf slope dominated by the intense southerly flow of the East Greenland current (Lavender et al. 2000). The Irminger Current carries relatively warm, saline water derived from the North Atlantic Current, and retroflects south of the Denmark Strait to join the East Greenland Current. This water mass becomes progressively cooler toward the south as it interacts with colder, fresher water of polar origin from the East Greenland Current, and with the oceanic waters of the Central Irminger Sea.

As northern euphausiids exhibit a high degree of plasticity in their life cycles and population dynamics in response to different trophic and environmental conditions, we might expect short-term, regional variation in euphausiid abundance, distribution and life cycles within the Irminger Sea that correspond with the distinct physical zones. A central objective of this investigation is therefore to address for the first time short-term, small scale variation in euphausiid abundance, distribution and growth in the region in relation to prevailing environmental characteristics such as temperature and food availability, which are key controllers of growth.

1.6.3. The trophic role of M. norvegica and T. longicaudata

Although the structure and functioning of high latitude pelagic food webs is similar across all latitudes, the key prey organisms for vertebrate predators vary between polar ecosystems (Smetacek and Nicol 2005). Crustaceans (predominantly Antarctic krill) are the main prey items in the south whereas mesopelagic fish (e.g. polar cod and myctophids) are in the north. This indicates that cold adaptation has not favoured

a specific food chain (Smetacek and Nicol 2005). However, euphausiids still have an important role in North Atlantic pelagic food webs, particularly *M. norvegica* and *T. longicaudata* that are important macroherbivores in terms of biomass (Figure1.4). Both these species consume phytoplankton and are predatory on calanoid copepods, particularly *Calanus finmarchicus* (Bamstedt and Karlson 1998; Falk-Petersen et al. 2000). These species are also major constituents in the diet of commercially targeted fish species, such as Redfish (*Sebastes* sp.), capelin (*Mallotus villosus*), herring (*Clupea harengus*) and whiting (*Merlangius merlangius*) (Astthorsson and Gislason 1997; Gonzalez et al. 2000; Sigurdsson et al. 2006; Skjoldal and Hassel 1991), squid (*Loligo* sp.) and Baleen whales (*Balaenoptera physalus*) (Macauley et al. 1995; Vikingsson 1997). Indeed, studies in the Barents Sea have identified a distinct predator-prey interrelationship between planktivorous capelin and euphausiids (Dalpadado and Skjoldal 1996). These authors observed a strong reduction in capelin stock that corresponded with a subsequent increase in the abundance and biomass of *T. longicaudata* and *vice versa*.

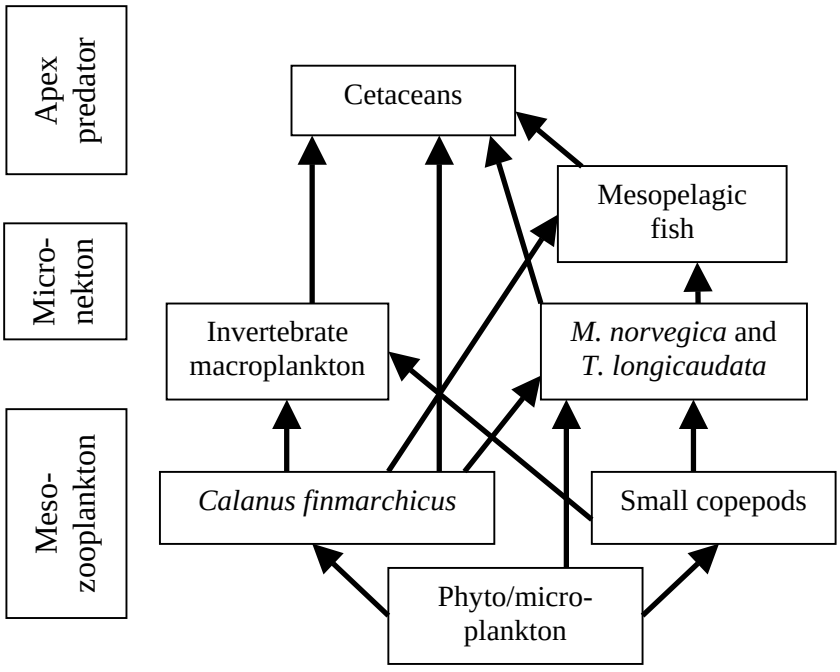

Figure 1.5. A simplified representation of the sub-Arctic food web.

The North Atlantic is subject to decadal-scale variations, including the North Atlantic Oscillation (NAO), which can have large impacts on the distribution and life cycles of ecologically important zooplankton species in systems that are exploited

commercially (Beaugrand 2003). Recent studies have detected large-scale changes ("regime shift") in the biogeography of calanoid copepods in the eastern North Atlantic and European shelf seas, with a northward extension of more than 10º latitude of warm-water species associated with a decrease in the number of cold water species (Beaugrand et al. 2002). These biogeographical shifts are related to both the increasing trend in Northern Hemisphere temperature and the NAO (Beaugrand et al. 2002). There is also increasing evidence that the impact of such climate-mediated biogeographical shifts in plankton could propagate up pelagic food webs because of tight trophic coupling (Richardson and Schoeman 2004). Future climate change (i.e. warming) is therefore likely to alter the spatial distribution of primary and secondary pelagic production, affecting ecosystem function and placing additional pressure on already-depleted fish and mammal populations (Richardson and Schoeman 2004; Smetacek and Nicol 2005).

The Irminger Sea is remote and until this study, there were no time-series data describing seasonal variation in euphausiid distribution, abundance and population dynamics in the region. Thus it has not yet been possible to address in detail seasonal variation in euphausiid distribution, abundance and growth. The few existing data from the Irminger Sea were collected from a single time of year (spring/early summer) using various sampling gears during the early 1930's (Einarsson 1945). Also, these data were collected from several different regions within the basin over a number of years. CPR data have provided valuable insight into the ecology of euphausiids in the North Atlantic (Lindley 1978; Lindley 1982), but these data are restricted to commercial shipping routes mainly outside of the Irminger Basin. The CPR is also limited to the upper 10 m of the water column and is size selective (Batten et al. 2003). Many late juvenile and adult euphausiids, such as *M. norvegica*, are too large to be sampled effectively by the CPR and they typically reside at depths below 400 m during daylight hours (Mauchline 1980a). Consequently, there is a pressing need for increased net haul data on the euphausiid component of the Irminger Sea ecosystem to provide a benchmark for further investigations into climate-mediated ecosystem change in the region and throughout the eastern North Atlantic.

1.7. Conclusions and aims of the investigation

High latitude pelagic ecosystems are ecologically important and are sensitive to over-exploitation of marine resources and climate change. However, our understanding of ecological processes and the possible impacts of such pressures in these regions are limited. There is a pressing need to quantify the distribution and abundance of key zooplankton groups, such as euphausiids, and to resolve the bio-physical mechanisms driving zooplankton patchiness at the most appropriate temporal (intra-annual) and spatial (within-basin) scales. Such information is vital for the implementation of robust ecosystem-based management strategies and for ameliorating the combined effects of climate change and marine resource exploitation. South Georgia and the Irminger Sea are both examples of high latitude pelagic ecosystems. Although these systems are different in many respects, they share some common environmental characteristics, such as low water temperature and high seasonality, and are similar in terms of the importance of euphausiids in the pelagic food web, ecosystem function and the scale of physical processes that impact zooplankton populations. South Georgia and the Irminger Sea are also unified in that they are both characterised by inter-annual, and possibly decadal scale, variability that may have a large impact on euphausiid abundance, distribution and life cycles. However, the physical processes driving such biological variation remain unclear. Understanding within-year variation is central to understanding change at a broader temporal resolution, but there are currently few data on euphausiids at high latitudes on sub-annual time-scales. This investigation therefore examines the krill-ocean component of high latitude ecosystems on an intra-annual time scale using data from South Georgia and the Irminger Sea. The investigation uses a combination of acoustic data from moorings and conventional ship-based platforms to quantify the timing, magnitude and controls of short-term, intra-annual variation in krill abundance at South Georgia. The study also uses net data to identify short-term, intra-annual variation in euphausiid abundance, distribution and population dynamics in the Irminger Sea in relation to basin-scale physical processes. By comparing and contrasting the two systems, the thesis then aims to provide new insight into the most important biological and physical factors controlling spatial heterogeneity in macrozooplankton abundance and distribution at high latitudes. The specific aims of the study were:

1. Devise and substantiate a robust method for monitoring intra-annual variability of Antarctic krill (*Euphausia superba*) abundance using moored instrument arrays (Chapter 2).

2. Quantify the timing and magnitude of short-term, ecologically significant, intra-annual variability in Antarctic krill abundance at South Georgia using moorings (Chapter 3).

3. Examine the key oceanographic mechanisms driving short-term, intra-annual variation in Antarctic krill abundance, and address the hypothesis that krill immigration to, and therefore at, South Georgia is mediated by influx of cold waters associated with changes in the position of the Sub Antarctic Circumpolar Current Front (SACCF) relative to the island (Chapter 4).

4. Ascertain seasonal changes in abundance, distribution, size and population dynamics of key euphausiids in the Irminger Sea, North Atlantic (Chapter 5).

5. Examine the important bio-physical controls of macrozooplankton spatial heterogeneity in high latitude ecosystems (Chapter 6).

2. Use of moored acoustic instruments to measure short-term variability in abundance of Antarctic krill[1]

2.1. Abstract

Upward-looking ADCPs (300 kHz) and echosounders (125 kHz) were deployed on moorings at South Georgia to measure abundance of Antarctic krill continuously over several months. Echoes from krill were identified using the theoretical difference in echo intensity at 300 and 125 kHz, and scaled to krill density using target strengths appropriate for krill in the region: krill size was determined from diet samples from furseals and penguins foraging near the moorings. A method using water flow past the moorings to convert time-based acoustic observations of krill to area-based abundance estimates was developed. Flow past the stationary moorings was treated analogously to motion along-track of a research vessel through a nominally-stationary body of water during a conventional survey. The moorings thus provide a Eulerian view of variation in krill abundance. This is ecologically instructive for South Georgia, where krill are generally passive drifters on currents and where temporal fluctuations in abundance have significant consequences for krill-dependent predators. Moorings were positioned on routine research vessel survey transects, and validity of the mooring method was assessed by comparison of mooring and vessel observations. Krill density estimates from the moorings were not statistically different from vessel estimates in adjacent time periods. A time series of krill density from a mooring revealed step-changes that were not seen during short-term vessel surveys. Moorings deliver data over time scales that cannot be achieved from research vessels, and provide insight to environmental factors associated with variation in krill abundance at South Georgia. Mooring data may aid ecosystem-based management.

[1]The work described in this chapter was published as part of: Brierley, A.S., **Saunders, R.A.**, Bone, D.G., Murphy, E.J., Enderlein, P., Demer, D.A., and Conti, S. 2006. Use of moored acoustic instruments to measure short-term variability in abundance of Antarctic krill. Limnology and Oceanography: Methods **4:** 18-29.

2.2. Introduction

Pelagic systems are variable over numerous scales of space and time (Haury et al. 1978; Murphy et al. 1988). Understanding the causes and consequences of this variability is an essential step towards understanding pelagic ecosystem function. At South Georgia, in the Atlantic sector of the Southern Ocean (54°S, 37°W), the food web is centred upon Antarctic krill (*Euphausia superba*), and temporal variability in local abundance of krill has major impacts on ecosystem function there. Acoustic surveys of krill abundance at South Georgia have revealed significant variation between years (over two orders of magnitude, from 2 to 150 g m^{-2} wet mass, between 1994 and 1998; (Brierley et al. 1999b). Years of low mean krill density (c. <10 g m^{-2}) result in significantly reduced reproductive success for krill predators such as Antarctic furseals and Gentoo penguins (Croxall et al. 1999), and poor condition of the commercially important Mackerel icefish (Everson et al. 1997). Understanding, and ultimately being able to predict (Brierley et al. 1999b), variability in krill abundance at South Georgia will be necessary before robust ecosystem-based management strategies for the region can be implemented.

South Georgia is remote and experiences often-hostile weather conditions. Logistic and financial constraints restrict the time over which data on the pelagic ecosystem can be gathered using conventional ship-based approaches. Although existing summer data (almost no winter data exist) show apparent year-to-year variation in krill abundance at South Georgia, few data are available on variation within years, and the possibility that apparent inter-annual variability is a temporal alias of shorter-term, intra-annual variation cannot be discounted. In fact, on the few occasions when more than one research cruise per year has made measurements at the island, marked within-year variations in krill abundance have been detected (for example 2 g m^{-2} wet mass in October 1997 cf. 21 g m^{-2} in January 1998; (Brierley et al. 1999a). Data from predators breeding ashore at South Georgia suggest that krill availability can vary significantly throughout the course of the breeding season (for example significant changes in the foraging behaviour of Antarctic furseals have been detected; (Mori and Boyd 2004), but a lack of corroborating independent at-sea observations has prevented direct verification of this. Evidence from elsewhere around Antarctica suggests that local krill abundance

can change substantially within seasons (1994; Siegel et al. 1998). Understanding the scale, timing and causes of such variation is key to understanding, managing and conserving the South Georgia pelagic marine ecosystem. Low krill abundance at the peak of the predator breeding-season, for example, could have far graver ecosystem consequences than would a krill scarcity during mid winter, and these two scenarios would have different implications for krill fishery management in an ecosystem context (Constable et al. 2000). Present at-sea sampling regimes could not resolve such short-term differences in krill abundance however, and it has been impossible so far to link predator breeding performance indices to krill abundance (i.e. to describe functional responses of predators to varying prey availability) because of the mismatch between the time scales of the vessel surveys (c. 2 week duration) and the breeding season (4 to 5 months) (Reid et al. 2005). Furthermore, it has not yet been possible to determine the causes of short-term changes in krill abundance at South Georgia. The krill population at the island is not self sustaining, and it has been suggested that abundance changes partly due to fluctuations in the position of the Sub Antarctic Circumpolar Current Front (SACCF) that acts as a conveyor belt transporting krill to South Georgia from the Antarctic Peninsula (Thorpe et al. 2004). The SACCF is a dynamic feature that retroflects around the eastern tip of South Georgia. When it meanders towards the northern shelf it may deliver krill to the island, in which case increases in krill abundance should be associated with the arrival of water with the properties (temperature and salinity) of the SACCF. To date, lack of contemporaneous oceanographic and krill abundance data has prevented this hypothesis from being tested empirically.

We deployed moorings at South Georgia to measure krill abundance and oceanographic parameters continuously and so gain insight to possible variations in abundance, and causes thereof, that could not be achieved with conventional ship based sampling. Use of moorings to investigate temporal variability in pelagic ecosystems is not new (Cochrane et al. 1994; Fischer and Visbeck 1993; Tarling 2003), and a forward look at priorities for zooplankton research (Marine Zooplankton Colloquium 2001) identified use of remote sensing tools such as acoustic moorings as key to future studies of zooplankton hotspots. To our knowledge, however, previous mooring-based studies have not attempted to scale the point observations they gather to account for variability in water flow past them. In regions where current velocity is not uniform, scaling for flow will be important because, to take an extreme example, a

period of apparent sustained high acoustic backscatter (planktic biomass) could be due to a single discrete aggregation in an otherwise empty background remaining stationary over the mooring: in that case the view from the mooring would be of continually high abundance, whereas the more widespread regional view would be of generally low abundance. In the case of krill, which are characterised by extremely patchy distributions (most biomass is in compact, high density swarms), setting mooring-based observations in a wider context is particularly important (predators, for example, cannot be expected to forage for our convenience directly over moored instruments), and we need to understand both temporal and spatial variation in abundance (Trathan et al. 1993). In this paper we report a method we have developed that uses the rate of flow of water past the mooring to scale time-based observations of krill abundance. Analysis of data from what we have called 'virtual survey transects' enables quantitative biomass estimates to be calculated. We describe analysis of data from a mooring deployed off shelf at South Georgia between November 2004 and January 2005 to illustrate our method. The method has potential wide application for studies of planktic ecosystems.

2.3. Materials and Procedures

Acoustic surveys are conducted routinely to estimate abundance of pelagic species such as herring, pollock and krill (Simmonds and Maclennan 2005). During these surveys, calibrated echo intensity data are recorded from pings transmitted downwards into the water column at regular intervals (typically 1 s) at one or more frequencies (typically 38, 120 and 200 kHz) from a research vessel progressing along pre-defined survey transects (typically at 10 knots). Each ping is time- and position-stamped (using GPS) and provides the volume backscattering coefficient (s_v, m^{-1}) for regular depth bins (the size of which depend upon the rate at which the echosounder samples the echo wave) down the water column. Further averaging down the water column or integrating along track leads to volumetric (eg Mean Volume Backscattering Strength (MVBS), S_v, dB re 1 m^{-1}) or areal (eg Nautical Area Scattering Coefficient (NASC), s_A, m^2 $n.mi^2$) measures of sound scattering that can be scaled using target strength (TS, dB re 1 m^2) to provide various measures of animal abundance. Target strength at a given frequency usually varies as a function of

animal size, and physical samples of the target species have to be obtained to determine size: this is usually achieved by net sampling. Net sampling also provides information on the species identity of acoustic targets: identifying the targets that cause echo returns is an essential step in determining single-species biomass estimates that are not biased by inclusion of echoes arising from other species. Substantial progress has been made recently in the use of echo intensities collected simultaneously at multiple frequencies from the same sampling volume for species identification (and sizing), and in some cases it is no longer essential that net samples be obtained (Horne 2000). In order to determine krill abundance estimates from moorings, mooring equivalents of each of the above steps have to be completed. The way in which we implemented these steps is described below.

2.3.1. Mooring location

Two moorings were deployed at on- and off-shelf locations to the north west of South Georgia (Figure 2.1) from RRS *James Clark Ross*. Moorings were first deployed in October 2002 and have remained more-or-less continually in place apart from brief periods (usually about 1 day, at approximately 4 month intervals, when they have been recovered for data download, battery replacement and servicing) to the present. On- and off-shelf locations were chosen because previous acoustic surveys had shown that krill abundances were different in the two zones (Trathan et al. 2003), and oceanographic conditions in the two regions are not uniform (Brandon et al. 2000). Both locations were within a box (the 'western core box') that was surveyed routinely as part of ongoing British Antarctic Survey (BAS) core research (Brierley et al. 1997) and, as far as possible (where bathymetry allowed), moorings were placed on standard survey transects within the box. The survey box itself was positioned to include foraging areas used routinely by air-breathing krill predators that breed ashore at Bird Island on the western tip of South Georgia, the location of a long-term BAS predator monitoring programme (Croxall et al. 1999). This methods paper reports analysis of data collected by the offshore mooring during a deployment between November 2004 and January 2005. Full analysis of the complete time series will be presented elsewhere.

2.3.2. Mooring design and instrument configuration

The design of the two moorings was essentially the same, with the exception that the anchor tether for the off-shelf mooring was longer. Moorings were anchored with ballast weights (railway wheels) to the seabed via acoustic releases, with the instrument packages floating a nominal 200 m below the sea surface.

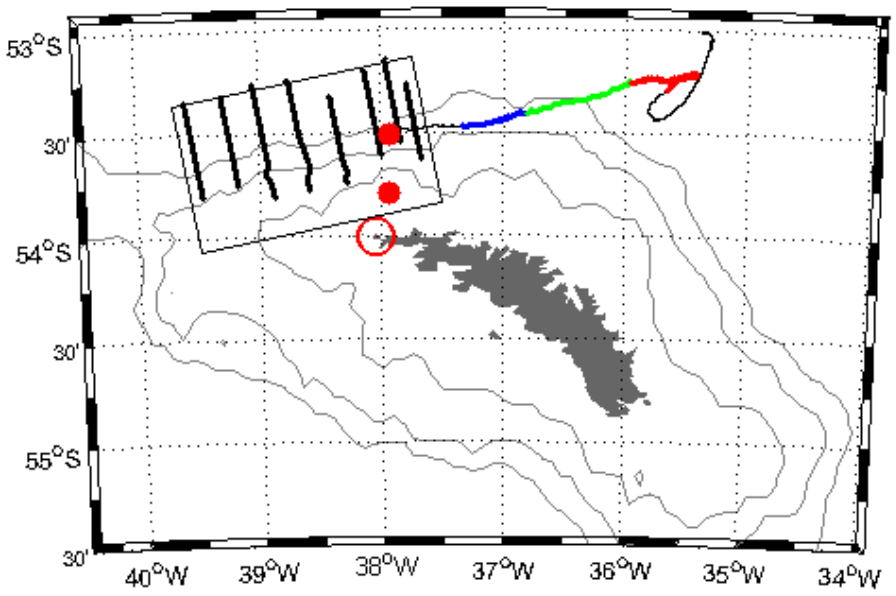

Figure 2.1. Map showing South Georgia and the surrounding bathymetry (200 m, 1000 m and 2000 m depth contours), the locations of the on- and off-shelf moorings (solid red dots), the bounds of the British Antarctic Survey western core box and portions of survey transects in water deeper than 200 m (only the four most eastern transects were considered in the ship-based analysis reported here), and the location of Bird Island (red circle) where predator diet sampling took place. The progressive vector plot (PVP) of water flow over the off-shelf mooring (in the 100 – 108 m depth horizon) for the duration of the deployment considered here is also shown (colours highlight portions of track during three separate density phases: red beginning; green middle; blue end: black sections are outwith analyses reported here). Although we show the entire PVP, we do not mean to imply that we think we can extrapolate to determine the exact historic trajectory over the whole period: this is an oceanographically very dynamic region (Murphy et al. 2004b). Rather we include the entire vector to provide a relative indication of the variation in water flow at the mooring site throughout the observation period. The variability that is apparent reinforces the need to scale temporal observations for spatial variability.

The seabed was at approximately 1300 m depth at the off-shelf location (requiring a 1100 m tether), and at approximately 300 m on-shelf (100 m tether). During the

deployment considered in this paper, the off-shelf mooring was at a depth of 226 m. Each mooring included a single-beam echosounder (ASL Environmental 125 kHz Water Column Profiler; hereafter WCP), an acoustic Doppler current profiler (RDI Workhorse 300 kHz; ADCP) and conductivity/temperature/depth logger (Seabird SBE37; CTD). The instruments were mounted in cylindrical apertures in a high-density syntactic foam flotation buoy (1.7 m diameter × 0.6 m depth; mass in air 636 kg; buoyancy 347 kg; CRP Group Ltd) (Figure 2.2), the size of which was determined by the buoyancy required to float the instruments and to maintain them in a stable position, without oscillation, in the current-swept environment off South Georgia (average prevailing current speed c. 10 cm s^{-1}). The ADCP and WCP were oriented to sample vertically upwards, and sampled from just above the mooring to the sea surface. Configurations for the ADCP and WCP during the deployment reported here are given in Table 2.1. These configurations were typical, and provided the highest-frequency data acquisition over the planned duration of the deployment that the manufacturers' specifications suggested available battery power and memory capacity could support. The CTD sampled just beneath the flotation buoy and recorded measurements every 4 minutes. In addition to the sampling instruments, the moorings were equipped with strobe lights and Argos beacons that helped us to find them at the surface during recovery.

2.3.3. Analysis of water column profiler backscatter data

The ASL Environmental WCP is a single-beam echosounder that has been developed from an instrument originally designed to measure draft of sea ice keels. It has an 18° 3 dB beam width. The WCP recorded echo intensity on a 0 to 255 linear scale. We converted these data to mean volume backscattering strength (S_v, dB re 1 m^{-1}) using an active version of the SONAR equation for distributed targets (Urick 1983):

$$S_v = 20\log N - G - OCV - SL + (20\log R + 2\alpha R) - 10\log(\tau\psi c/2)$$

where R is range (m), N is the recorded WCP count, OCV is the transducer receiving response (open circuit voltage, dB re 1V/μPa), SL (source level, dB re 1 μPa) is the transmitted signal intensity, α is the absorption coefficient (dB m^{-1}), c is sound

velocity (m s^{-1}) [α and c were calculated using temperature and salinity values logged by the mooring CTD], ψ is the equivalent 2-way beam angle (0.01172 steradians), τ is the pulse length (s), and G is the receiver gain (dB). OCV and SL are instrument specific constants and were provided by the manufacturer. The gain function G was determined using measured Time Varied Gain (TVG) curves provided by the manufacturer. Limitations in the WCP electronics meant that that gain function did not quite conform to the standard 20logR, and we determined G using a 6-term range-dependant polynomial model of the manufacturer's measurements. The WCP was calibrated with reference to echo intensities recorded from a standard target during a calibration exercise in Stromness Bay, South Georgia (WCP at c. 10 m depth).

2.3.4. Analysis of acoustic Doppler current profiler data

The RDI Workhorse Sentinel ADCP is used widely for oceanographic and bioacoustic research. It has 4 beams, each with a 3.9° 3 dB beam width, which are orientated with a slant 20° off vertical. The ADCP recorded echo intensity on a 0 to 255 Automatic Gain Control (AGC) count scale. We converted AGC to S_v using the version of the SONAR equation presented by Deines (1999):

$$S_v = c + 10\log((T_x + 273.16)R^2) - L_{DBM} - P_{DBW} + 2\alpha R + K_c(E-E_r)$$

where R is the (slant) range to the sample bin (m), c is a sonar-configuration scaling factor (that includes the system-source level, transducer directivity, transducer efficiency and the Boltzmann constant that is applied to scale thermal noise to an absolute level; 143.5 dB for the Workhorse Sentinel); T_x is the temperature at the transducer (^oC); L_{DBM} is 10log (transmit-pulse length) (m), P_{DBW} is 10log(transmit power) (dB re 1 W), α is the absorption coefficient (dB m^{-1}), K_c is a beam-specific sensitivity coefficient (supplied by the manufacturer), E is the recorded AGC, and E_r is the minimum (background) AGC recorded. We used beam-averaged data because the four beams together give a better signal-to-noise ratio than individual beams, and provide information from a larger sampling volume.

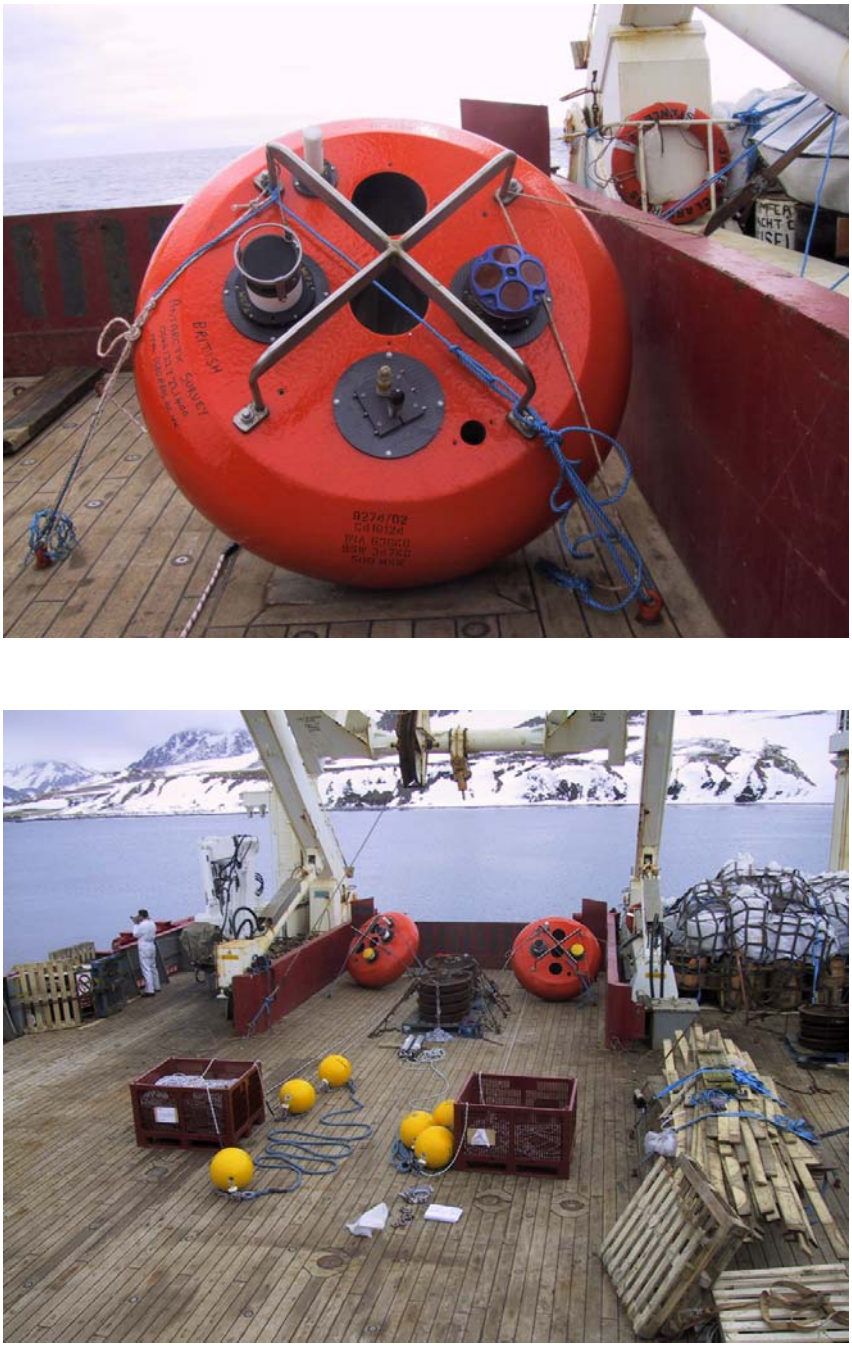

Figure 2.2. Photographs showing (a, upper pane) the mooring buoyancy float and instruments (ADCP right, WCP left, Argos beacon top, radio and light beacons bottom. The CTD is beneath the float and hence not visible), and (b, lower pane) both moorings on the after deck of RRS *James Clark Ross* (the off-shelf mooring is on the left hand side, and has substantially more tether in the square basket than does the on-shelf mooring). The instrument floats, railway-wheel ballast and acoustic releases are lying beneath the A-frame.

2.3.5. Preparation for acoustic identification of krill

The moorings were equipped with acoustic devices (ADCP and WCP) operating at two frequencies so that a frequency-difference technique could be used to identify echoes arising from krill and discriminate them from echoes from other targets. The proportion of sound energy backscattered from a target at a given frequency is a function of numerous physical properties of the target, including size, shape, orientation, and the ratios of the density of the target to the density of sea water, and of sound velocity in the target to sound velocity in sea water. Different targets (eg plankton types such as euphausiids, copepods and salps) may backscatter different proportions of energy because they have different physical properties (eg euphausiids are larger than copepods, and are denser than salps). Over a range of frequencies, different plankters have characteristic scattering responses, such that species can often be distinguished on the basis of their dual- or multi-frequency 'fingerprint'. At South Georgia, where plankton species diversity is quite low, and where the majority of krill biomass is usually contained in high-density swarms, this approach has proved effective (Brierley et al. 1998b; Madureira et al. 1993; Watkins and Brierley 2002).

Table 2.1. Instrument configurations for the water column profiler (WCP) and acoustic Doppler current profiler (ADCP).

Instrument	Frequency	Sampling rate	Range bin	Pulse length	Blank after tx
WCP	125 kHz	1 ping every 2 minutes	0.5 m	600 μs (= 8.72 m @ 1453 m s^{-1})	0 m
ADCP	300 kHz	7 ping ensemble every 4 minutes	8.0 m	560 μs (= 8.13 m @ 1453 m s^{-1})	1.76 m

S_v data from both the ADCP and WCP were loaded into SonarData Echoview software to enable them to be processed together, as follows. Firstly regions of bad data (times when instruments were pinging on deck before deployment and descending to their moored depths; depths in 'blank after transmit' and near-surface dead zone; periods of interference) were marked and excluded from further analysis. The depth range sampled effectively by the mooring during this deployment was approximately 20 m to 210 m. Second, TVG-amplified background noise was

removed from each dataset (Watkins and Brierley 1996). Third, the WCP data were re-sampled (averaged in the linear domain) on to a depth/time grid corresponding to the sampling resolution of the ADCP (8 m × 4 minutes): this enabled frequency differences from equivalent time periods to be determined.

2.3.6. Krill length frequency

We sampled krill in the vicinity of the mooring using a rectangular midwater trawl with a square 8 m^2 mouth opening (RMT8) just prior to the mooring deployment (n = 157, mean length = 44.2 mm). Krill were also obtained from diet samples of Antarctic furseals and Macaroni penguins breeding ashore at Bird Island (n = 478, mean length = 52.6 mm). Both of these species forage in the vicinity of the moorings. It has been shown previously (Reid and Brierley 2001) that sizes of krill in predator diet samples are representative of the regional krill population length frequency distribution, and thus that they can be used to infer acoustic target strength (TS).

2.3.7. Ventral-aspect TS of krill at 125 and 300 kHz

Conventional ship-based acoustic surveys detect animals from above with downward-facing echosounders that sample echoes arising from the animals' dorsal surfaces. Conversely, the instruments on our moorings sample from beneath and detect sound scattered back from the ventral surface. We used the Demer and Conti (2003) stochastic distorted-wave Born approximation (SDWBA) model to determine ventral aspect 125 and 300 kHz TS for krill with the length-frequency distributions (from net and predator samples) apparent during the deployment. The model was evaluated with a generic krill shape comprised of 14 cylinders (following Mcgehee et al. 1998), and an empirically-determined standard deviation of the phase variability of $\sqrt{(2)}/2$ radians (Demer and Conti 2003). Demer and Conti (2005) inferred that krill typically adopt a mean orientation 15° (tail down) off the horizontal (standard deviation 5°). The WCP was oriented vertically upwards and so, using the Demer and Conti (2005) model coordinate system (head = 180°, tail 0° or 360°, dorsal surface 90°, ventral surface 270°), would impinge upon typical krill at a mean of 285° (±5° SD). The

ADCP has 4 beams (20° slant) and this serves to broaden the range of angles at which krill might be 'viewed' to 265° to 305° (±5° SD). Variation of TS by angle is shown for the length frequency distribution of krill from the net sample in Figure 2.3. We calculated the average TS at 125 kHz and 300 kHz over appropriate angular ranges for each instrument (Table 2.2). We also calculated the maximum and minimum differences in echo intensity at 125 and 300 kHz over these ranges, and used this difference range in Echoview to generate a mask to select those 8 m × 4 minute acoustic data bins within that range believed to contain krill.

Table 2.2. Target strengths (TS per individual krill) at each of the survey frequencies and observation angles, and frequency differences indicative of krill, averaged over the krill length frequency distribution determined by net sampling before the mooring deployment.

Instrument	Frequency kHz	Angular range degrees	TS mean dB	TS max dB	TS min dB	Krill ID range (S_v hi - S_v lo) dB
ADCP	300	255 - 315	-67.21	-59.52	-77.48	-14.77 to +14.53
WCP	125	275 - 295	-69.29	-62.70	-74.05	
EK60	120	dorsal aspect	-74.20	-71.28	-78.19	+3.10 to +8.72
EK60	38	dorsal aspect	-79.54	-74.38	-86.91	

2.3.8. Construction of 'virtual survey transects'

An important parameter in the calculation of krill density from a shipboard acoustic survey is the length of the survey transect sampled. This is used to scale the observed krill density values to the unit area of water sampled, and ultimately to calculate a regional mean density (Jolly and Hampton 1990). In order to calculate robust mean density estimates from the moorings, the rate of flow past the mooring has to be considered. We used the ADCP velocity measurements to determine flow. The north and east velocity components for bin 14 (depth = 100-108 m) were used to construct progressive vector plots (PVP) with the Matlab 'Fathom' toolbox (available for download from the website of the author, David L. Jones, Department of Marine Biology and Fisheries, University of Miami, USA, at http://www.rsmas.miami.edu/personal/djones/).

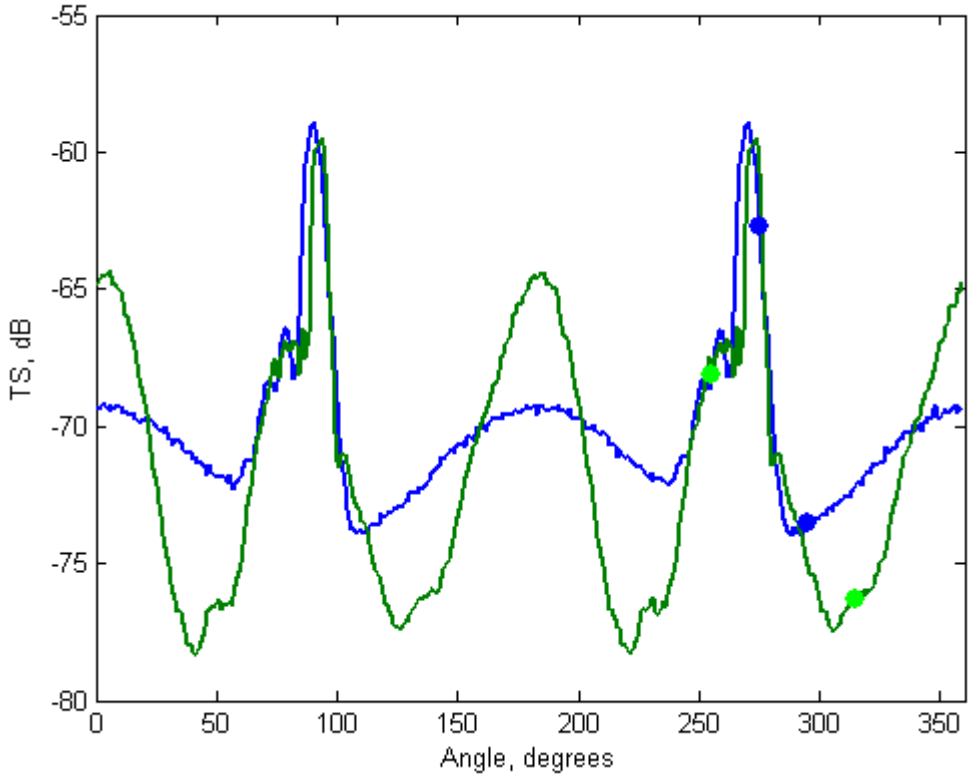

Figure 2.3. Target strengths at 125 kHz (WCP, blue line) and 300 kHz (ADCP, green line) for krill (averaged over the length frequency distribution detected by net just prior to the mooring deployment) as a function of angle. The extreme bounds of the sections of the curves corresponding to the limits of the ranges of ventral aspect angles viewed from the moorings are marked with filled circles.

These plots provide a Lagrangian display of Eulerian measurements, and can be considered analogous to the cruise track of a research vessel conducting an acoustic survey through a nominally-stationary body of water. The 100-108 m depth range was chosen as approximately the mid point of the observational range (c. 200 m to 20 m) and because data quality was consistently good in this bin (% good > 25). This depth is also at approximately the centre of the distribution range of krill swarms at South Georgia in daylight (Godlewska 1996; Taki et al. 2005) and, as such, water movement at this depth interval is likely to be representative of the conditions encountered *in situ* by most krill sampled at the island. We could find no evidence of sheer above the offshore mooring, and there was no significant variation in velocity with depth over the range where %good remained high (bins 1 to 16): for observations at mid day on alternate days throughout the deployment (n = 20), mean velocity at bin 14 was 11.0 cm s^{-1} (SD 7.2) and the mean over all bins was 10.3 cm s^{-1} (range 9.2 to 11.4 cm s^{-1}). Our choice of depth for PVP construction is unlikely to have biased our

conclusions. In locations where sheer is strong, however, it may be advisable to determine a mean velocity over the entirety of the depth range occupied by the organism of interest, and use this mean to construct the PVP.

Water velocities are determined by ADCPs using echoes from particles in the water (including plankton) on the assumption that the particles are drifting passively and that particle motion is due entirely to the motion of the water. If the particles are moving independently of the water then particle motion may bias inferred water velocity. It has been shown, for example, that fish movement can bias velocity measurements (Plimpton et al. 1995) and indeed ADCP data have been used to infer fish motion (Demer et al. 2000). In order to determine if krill motion might bias our estimation of water velocity (and thus our 'virtual survey transects') we extracted velocity measures from within 20 krill swarms (detected during daylight) chosen at random throughout the deployment and from empty water immediately adjacent to each the swarm and conducted paired t-tests to see if differences could be detected.

The PVP data were transformed to equivalent latitude and longitude co-ordinates relative to the position of the mooring using The Geographic Calculator (V 3.09), a Universal Transverse Mercator projection and zone 24 S / 42°W to 36 °W (see Figure 2.1). These latitude and longitude data were loaded in to Echoview as if they were a ship's GPS data, and linked by time to backscatter data.

2.3.9. Calculation of krill density from mooring data

Echo integration (in Echoview) of echoes identified on the basis of their frequency difference as arising from krill enabled NASC values attributable to krill to be determined at regular (we chose 30 minute) intervals throughout the deployment. The dB difference filter identified 26.7% of integration cells as containing krill (these cells contained 93.3% of all backscattered echo energy). Echoes from krill were scaled to krill density (g m^{-2}) using the target strength appropriate for each instrument for the length frequency of krill sampled by predators during the mooring deployment (separate density estimates were calculated at 125 and 300 kHz. $TS_{predators}$ 300 kHz = -43.83 dB kg^{-1}, $TS_{predators}$ 125 kHz = -44.92 dB kg^{-1}), generating time-series of krill

density at half-hourly intervals throughout the deployment. Diel vertical migrations were apparent in most echograms at dawn and dusk (approximately 06:00 and 23:00 Z for the middle of this deployment) and between these times, during hours of darkness, much of the plankton was lost to the near-surface deadzone that it was not possible to sample acoustically (Ona and Mitson 1996). Data from these periods were therefore discarded for further analysis. For each daily period (06:00 – 23:00), individual half-hour krill density values were multiplied by the flow distance for that half-hour period: flow distance was calculated using spherical trigonometry from the ADCP-derived 'GPS' position for the start and end of each interval. The daily mean krill density was then determined as [sum(density × distance)] / [sum(distance)]. This is exactly equivalent to the treatment of ship survey data to calculate mean transect density (Jolly and Hampton 1990). Longer-term means for multiple daily periods were calculated as the mean of days within the period, weighted by the sampling distance for each day: again this is equivalent to the Jolly and Hampton (1990) method for calculating strata means from data from several transects.

2.3.10. Calculation of krill density from ship data

Acoustic surveys were conducted by RRS James Clark Ross along the standard BAS core box transects (Figure 2.1) using a calibrated Simrad EK60 echosounder operating at 38 and 120 kHz (hull-mounted transducers, downward facing) before mooring deployment and after mooring recovery. Krill were identified on the basis of the expected dB difference between dorsal aspect echoes at 38 kHz and 120 kHz (see Table 2.1) (Demer and Conti 2005). Echo integration was used to generate 120 kHz NASC values for krill at 137 m intervals along track (137 m was the mean flow distance past the mooring in an half hour interval) over the depth range equivalent to that sampled by the mooring (20 m to 210 m). Data were excluded from portions of the transect land-ward of the 210 m depth contour because we have seen previously that mean krill densities on-shelf are different to densities off-shelf (eg Trathan et al. 2003): calculation of ship-based density estimates from on- and off-shelf data would not facilitate a like-with-like comparison with the off-shelf mooring. NASC data (120 kHz) from the ship survey before the mooring deployment were scaled to krill density using a dorsal aspect target strength appropriate for the krill length frequency

determined from the net sample (TS_{nets} 120 kHz = -42.76 dB kg^{-1}); data from the ship survey after the mooring deployment were scaled using the TS appropriate for the predator derived length frequency distribution (TS_{preds} 120 kHz = -43.71 dB kg^{-1}; no net sampling was conducted during the post-mooring ship survey). 120 kHz TS values were calculated form the TS-to-krill length relationship given by Demer and Conti (2005) that is a polynomial approximation of the SDWBA model output. Krill densities from each 137 m interval were used to generate weighted transect and box means using the method of Jolly and Hampton (1990).

2.4. Assessment

2.4.1. Mooring acoustic observations

The mooring deployment considered here was from November 25 2004 to January 10 2005. The ADCP logged data throughout this period, but a battery failure caused the WCP to stop on December 20. Krill identification using the dual-frequency technique was possible for a 26-day period. During that time numerous krill swarms were detected (Figure 2.4) in the water above the mooring. The maximum mean volume backscattering strengths detected by the ADCP (4-beam average) and WCP were in the order of -46.5 dB, equating to a krill numerical density of roughly 150 animals per m^3. These values are below saturation (no values of 255 were recorded) and the dynamic ranges of both instruments were thus adequate for evaluating krill swarms with the packing density prevailing during this deployment.

Mean flow velocity (at 100-108 m) during the deployment was 7.6 cm s^{-1}, leading to a mean sampling distance of 137 m for a 30-minute interval, but velocity was not constant and sampling distance ranged from 5 m to 403 m. This variation illustrates well why backscatter values need to be scaled by sampling distance to calculate unbiased mean density estimates. This is further illustrated by the meander in the PVP in the period after the WCP battery failed (black line, Figure 2.1). Although flow velocity varied throughout the deployment, we could find no evidence for differences in velocity within krill swarms compared to in empty water, and thus have no reason to believe that the presence of krill biased our inferred sampling distances.

Within the 20 swarms (mean ADCP echo intensity -55.9 dB, mean depth 87 m, depth range 53 to 150 m) mean velocity was 11.6 cm s^{-1} (range 3.3 to 21.9 cm s^{-1}). Outside the swarms, at the same depth, mean velocity was also 11.6 cm s^{-1} (range 2.3 to 30.3 cm s^{-1}). Paired sample t-tests failed to detect any significant difference in velocities within and without swarms (n = 20; pre swarm cf. in swarm P = 0.44; in swarm cf. post swarm P = 0.35) and it thus seems unlikely that the presence of krill swarms would have biased our estimates of sampling distance.

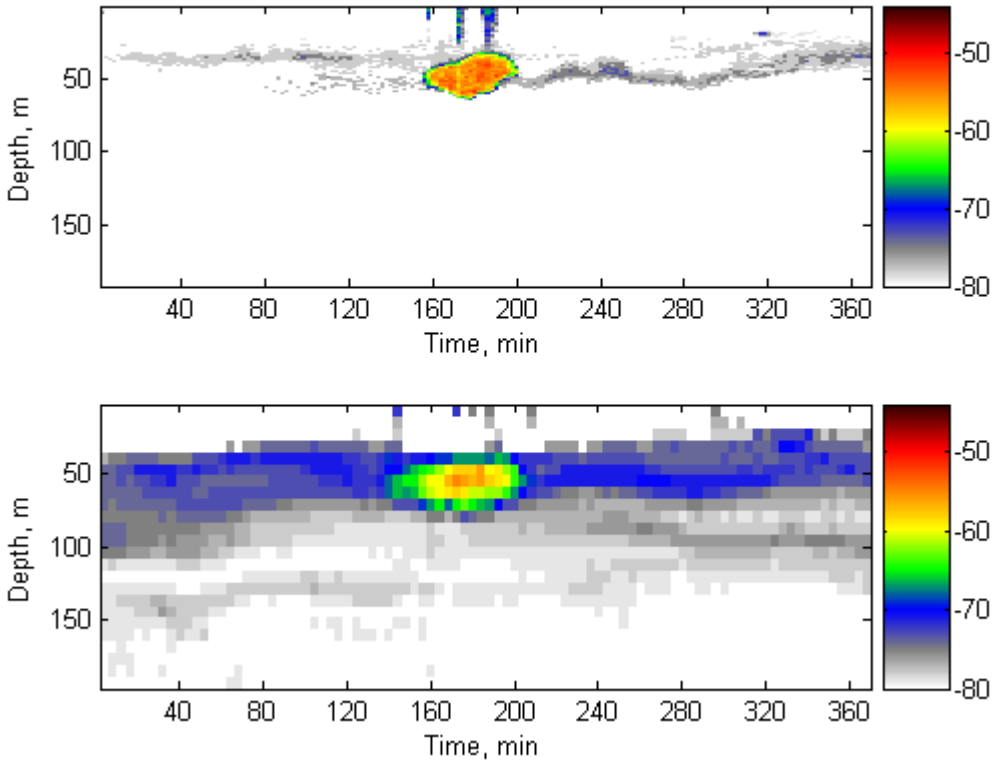

Figure 2.4. Echograms showing a krill swarm detected simultaneously by the WCP (upper panel) and ADCP (lower panel). Colour bar shows mean volume backscattering strength (S_v), dB. The swarm was identified as krill on the basis of the difference in echo intensity between frequencies. Note the finer resolution in the WCP echogram due to the more frequent time and depth sampling. Time 0 = 16:30 Z, December 9 2004.

The time series of krill density (from the WCP) for the 26-day period is presented in Figure 2.5. A 24-point running mean through this time series (12 hourly) has a clear daily cyclicity, with low night-time values punctuating generally higher day time values. This is in part a consequence of krill migrating upwards into the surface dead zone at dusk and downwards away from the surface at dawn. There may also be a

tidal component to this variability (maximum power in the time series is at 14.8 hours): previous studies have reported an impact of tidal flow on euphausiid aggregation (Cotte and Simard 2005). The time series also shows prominent step-changes after 6 days (November 30) and 12 days (December 6) that divide it into three distinct density periods. Using the flow vectors over the mooring each day to construct daily (daylight only) 'virtual transects' and to weight daily mean density estimates in a manner analogous to that advocated by Jolly and Hampton (1990) for conventional survey transects, weighted mean krill densities (and standard deviations) for each period were calculated as 29.7 g m^{-2} (SD 12.8), 5.8 g m^{-2} (SD 2.8) and 33.6 g m^{-2} (SD 11.3) respectively using WCP data.

2.4.2. Comparison of WCP and ADCP backscatter

Successful implementation of a dual-frequency species identification technique requires that data at both frequencies are accurate. Calibration data for the WCP were collected with the standard target technique used routinely to calibrate ship's scientific echosounders (Foote et al. 1987), but calibration was conducted near-surface (10 m) and not at the c. 200 m operating depth, and depth may influence calibration (Dalen et al. 2003). The slanted beams of the ADCP are difficult to calibrate using standard target techniques and we were reliant on data from the manufacturer, ambient temperature information and the Deines (1999) equation to determine backscatter from the ADCP. Given our *a priori* uncertainty in calibration, we conducted a regression analysis to compare the krill densities determined from the ADCP measures of backscatter to those from the WCP. Considering all 1216 30-minute observation periods throughout the deployment,

$$\text{ADCP density} = 0.79\ \text{WCP density} + 28.89\ (r^2\ 0.76,\ P < 0.0001)$$

Confidence limits (95%) for the slope and intercept are 0.77 to 0.82 and 25.71 to 32.09 respectively. Substituting the WCP mean krill density (21.18 g m^{-2}) into the regression equation gives a ratio of ADCP density to WCP density of 2.15:1, which equates to a 3.3 dB difference between instruments. This difference, as expressed at the level of density, is a function not only of instrument calibration (change in depth

from 10 m to 200 m might cause around 0.5 dB change in WCP calibration, cf. (Dalen et al. 2003) but also of target strength (in turn a function of krill length-frequency and orientation). As such, a between instrument difference of just 3.3 dB is very pleasing, especially since we might anyway expect the ADCP to detect more krill swarms

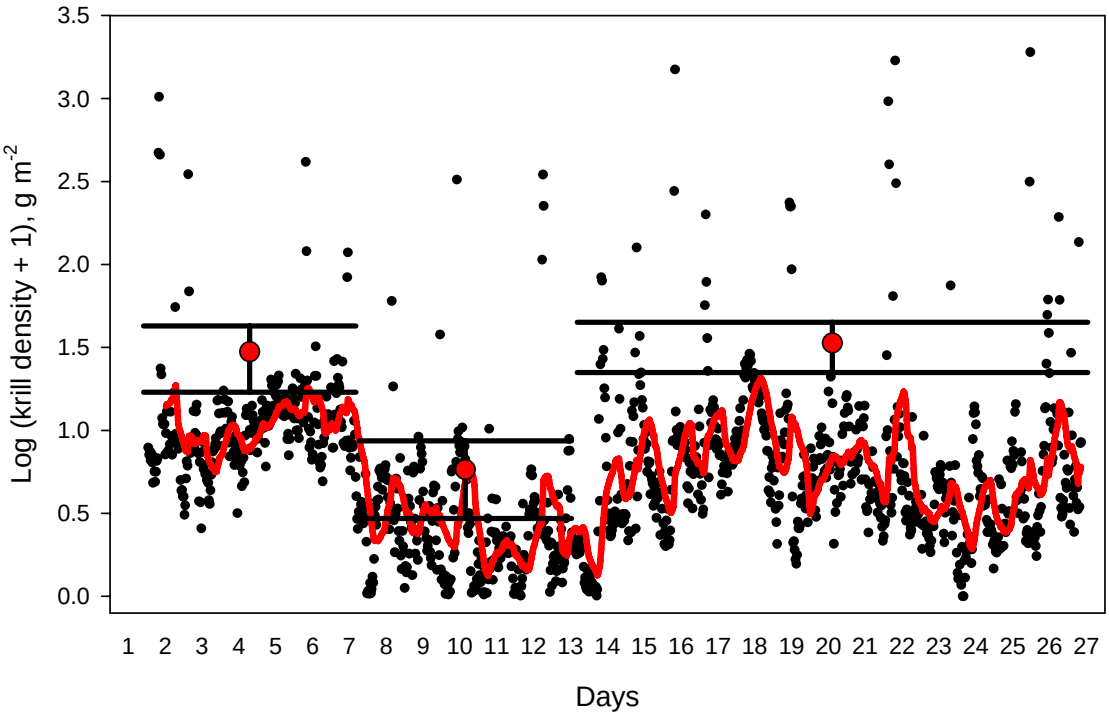

Figure 2.5. Time series of (log_{10}) krill density from the WCP, a 24-point moving average (of the log), and means (red circles, ± 1 SD error bars) for the 3 distinct density periods (first 6 days, middle 6 days, final 14 days). Day 1 starts 00:00 November 25 2004. The range of individual half-hour density values is high, as is usual for acoustic surveys of krill density, and much of the biomass is contained within relatively few high-density swarms.

(hence more biomass) since it is sampling a broader total area than the WCP (4 beams each 20° off vertical cf. one single vertical beam) and might detect swarms that pass outside the WCP sampling volume.

2.4.3. Comparison of mooring and ship

The moorings make measurements of krill at single points in the ocean. In order for us to have confidence that mooring-derived time series of krill abundance are representative of changes over a broader area, an area for example that might be

relevant to foraging predators, we need to examine mooring observations in context with more widespread (yet temporally restricted) observations. Conventional ship based acoustic surveys provide such data. Krill density in the South Georgia western core box is assessed by surveys of 10 transects each 80 km long and on average 10 km apart. At a survey speed of 10 knots, two such transects can be surveyed per day in daylight. Surveys are conducted in daylight only to avoid negative bias that would otherwise be caused as krill migrate to the near surface zone at dusk (this zone is not sampled by the ship's echosounder) (Demer and Hewitt 1995). We used standard protocols (eg Brierley et al. 1997, 1999b) to determine krill density from the four survey transects closest to the mooring from the surveys immediately before and after the mooring deployments, and considered mooring-derived krill densities in this context. Before the mooring deployment (RRS *James Clark Ross* cruise JR107) the mean krill density was 73.2 g m^{-2} (SD 21.7), and after the cruise (JR116) the mean was 24.1 g m^{-2} (SD 8.6). Cruise values are not statistically different from the densities derived from the mooring data at the start and end of the deployment (2 sample t-test between 4 ship transects from the pre-deployment survey and first 6 days mooring observations P = 0.18; 2 sample t-test between 4 ship transects from the post-deployment survey and last 14 days mooring observations P = 0.58).

2.5. Discussion

The step changes in krill density apparent in the mooring-derived time series after November 30 (from mean 29.7 g m^{-2} to mean 5.8 g m^{-2}) and December 6 (from mean 5.8 g m^{-2} to mean 33.6 g m^{-2}) are, to our knowledge, the first instances that abrupt changes in krill density have been detected directly at sea. Changes such as these had been hinted at by abrupt changes in predator foraging behaviour but, because of previous sampling limitations, had not been observed directly. The analyses reported here thus demonstrate clearly that the moorings meet the defined need, that is to gather data able to resolve short-term fluctuations in krill density. The high-to-low change in krill density apparent in the early part of the krill-density time series would be sufficient to change our opinion, in terms of interpretation of conventional ship-based observations, that the 2004/05 summer season was one of adequate krill availability for predators to the opinion that it was a season of poor krill availability.

This illustrates well why it has so far proved impossible to link krill abundance and predator breeding performance (Reid et al. 2005): if changes such as these are typical of most breeding seasons then single ship-based snapshots of krill availability may not provide a krill abundance estimate that is a good reflection of the predator's view of krill availability. We hope that ongoing analyses of longer time-series of mooring data – using the methods described here – will provide insight to the time scale of variability over multiple seasons. In the meantime, we must continue to attribute with caution changes in predator behaviour to changes in krill availability as indicated by existing ship-based time series of krill density. Ultimately, of course, it will be important to understand both temporal and spatial variability, and the causes thereof, if we are to progress to the point where we can predict changes in krill abundance at South Georgia and establish ecosystem-based management procedures that are responsive to such changes. Ship-based and mooring-based data will therefore be essential to obtain spatially and temporally extensive views on the South Georgia ecosystem.

The moorings provide new insight to the physical processes associated with the short-term changes in krill density at South Georgia. The changes in krill density reported here after November 30 and December 6 coincided with abrupt changes in water temperature (from c. 1.3°C to 1.1°C and back to 1.3°C, as detected by the mooring CTD) and velocity (from c 7 cm s^{-1} to 12 cm s^{-1} and back, as detected by the ADCP). It is not the purpose of this paper to present an in-depth analysis of the oceanographic causes of such changes, but they could be indicative of the passage of a front or eddy over the mooring. Inspection of the progressive vector plot from ADCP velocity data (Figure 2.1) shows that flow direction is not constant. Ward et al. (2002) reported the presence of two fronts on a transect running 160 km north east from South Georgia. They suggested that the fronts, which they considered to be two sides of a meander in the SACCF, exhibited higher velocities than surrounding water and that the SACCF water was cooler. It is possible that the mooring has detected a temporal manifestation of the changes observed spatially by Ward et al. (2002). Again, analysis of our longer mooring krill-density time series, and full consideration of the oceanographic data collected simultaneously, may provide a clear view of the

oceanographic changes that presage changes in krill abundance at South Georgia, and provide completely new insight to the hitherto unobserved winter period.

2.6. Comments and recommendations

South Georgia is a particularly hostile environment for mooring deployment. Icebergs frequently pass by and can remain for periods of many months if they become grounded. The moorings described here were designed to survive iceberg collisions, and did so on numerous occasions. The CTDs recorded several instances when the moorings were knocked downwards by the passage of a berg, only to float back to the original depth once the berg had drifted by. The robust nature of the moorings makes it likely that they would survive deployment in most other oceanic or lake locations. As long as an acoustic signature of the target species were known, it should therefore prove possible to use the method we describe here to assess temporal variations in abundance of most passively-drifting pelagic species.

The acoustic instruments on the moorings gathered data that provide plausible estimates of krill density that are consistent with ship based estimates in adjacent time periods. Krill density at South Georgia can however sometimes be very high (>150 g m^{-2}) and on these occasions very high density swarms are detected during ship-based surveys. Although the ADCP and WCP were not saturated during the deployment reported here, they may well have been had swarms of very high density been present. (Hamner and Hamner 2000) suggest numerical densities of up to 64000 krill per m^3 are possible, and these would provoke S_v values of around –20 dB. Although ADCPs can provide quantitative estimates of backscatterer density in some circumstances (Lee et al. 2004), this is not the principal purpose of the instrument and they do not always deliver values directly equivalent to those obtained by scientific echosounders (Brierley et al. 1999b). This, and the fact that they cannot easily be calibrated *in situ* (although we understand absolute calibration is now possible; Eberhard Fahrbach, Alfred Wegener Institut, pers. comm. 2005), leaves these instruments less than ideal for quantitative backscatter measurement. The ADCP is however essential for obtaining the current velocity measurements that are an integral component of the method reported here. Given unlimited finances, we would choose to equip the

moorings with purpose designed scientific echosounders that have documented calibration stability and high dynamic range (such as the EK60 used on the ship; these instruments have been housed for remote deployment under battery power), and to have at least two echosounder frequencies on the mooring in addition to the ADCP. Frequencies would be chosen so that uncertainty in krill orientation had less of an influence on target strength (see Figure 2.3) and thus density calculation. For use in other environments, on different target species, operating frequency could be chosen to best meet the compromise between resolution, range and species discrimination.

Although the moorings survived iceberg strikes, the off-shore mooring fared less well on one occasion in an encounter with fishing gear. Longliners operate along the shelf break, deploying baited hooks for Patagonian toothfish. On May 12 2003 a transmission from the Argos beacon on the off-shelf mooring alerted us to the fact that the mooring was on the surface. The mooring was eventually recovered for us by a fishing vessel operating in the area, and it seems likely that it was dragged to the surface after becoming entangled in a long line. In future we may opt to place the off-shelf mooring further away from the shelf-break, out of the zone targeted by fishing vessels.

To conclude, although acoustic data collected from moorings present some unusual challenges for analysis, they provide a window of observation onto pelagic systems not open from conventional research vessels. At South Georgia, they have provided data giving a completely new insight to the function of the coupled biological-physical marine system. We believe that incorporation of mooring data to regional ecosystem analyses will lead to much improved understanding of ecosystem function there: moorings will likely deliver equally new insight to ecosystem function elsewhere, and we encourage our colleagues to consider this approach.

3. Intra-annual variability in the density of Antarctic krill (*Euphausia superba*) at South Georgia, 2002-2005: within-year variation provides a new framework for interpreting previous 'annual' estimates of krill density[2]

3.1. Abstract

Upward-looking acoustic Doppler current profilers (300 kHz) and echo sounders (125 kHz) were deployed on moorings on- and off-shelf to the northwest of South Georgia between 14 October 2002 and 29 December 2005 to measure density of Antarctic krill and environmental parameters continuously. A distinct seasonal pattern in krill density was detected that recurred consistently over all 3 years. Krill densities in winter were predominantly low (mean = 18.7 g m^{-2} SD = 24.3) but rose substantially by summer in each year (mean = 89.5 g m^{-2} SD = 64.2). A sinusoidal regression model (period = 52 weeks) with time as the independent variable explained 64% of the observed week-to-week variation. Mooring estimates of krill density were not statistically different ($P>0.05$) from estimates derived from standard ship-based krill surveys in adjacent time periods, suggesting that the mooring point-estimates were representative of krill density in a wider spatial context (ship surveys cover c. 100 x 100 km). Mooring data were used to explore whether high frequency temporal variation (i.e. within-year) could have led to the perceived between-year variation in krill density arising from previous summer surveys in the South Georgia western core box region between 1990 and 2005. Comparison of these 'snap-shot' ship survey estimates with the observed pattern of within-year variability showed that some of the apparent 'year-to-year' variation could be attributed just to sampling on different dates of the year (e.g. November cf. February). However, there were some survey estimates that were significantly different ($P<0.01$) from the regression-predicted within-year variation. Years that stand out for markedly low krill density (i.e. densities below the range expected due to intra-annual variation) were 1993/94, 1998/99 and 1999/2000. Moorings provide valuable data that could be important for ecosystem-based management at South Georgia because, for example, they will enable predator-prey functional responses to be explored there for the first time at appropriate temporal scales, and will enable hypotheses relating variation in krill abundance to physical oceanographic variability to be tested.

[2]The work in this chapter was presented at the 2006 CCAMLR WG-EMM meeting as: **Saunders, R.A.,** Watkins, J.L., Reid, K., Murphy, E.J., Enderlein, P., and Brierley, A.S. 2006. Intra-annual variability in the density of Antarctic krill (*Euphausia superba*) at South Georgia, 2002-2004:within-year variation provides a new framework for interpreting previous 'annual' estimates of krill density (Document WG-EMM-06/25). The chapter is also in press for the journal CCAMLR Science.

3.2. Introduction

Acoustic surveys conducted during brief periods (typically 2 weeks) over the past 2 decades at South Georgia have revealed significant variation in the abundance of Antarctic krill (*Euphausia superba*) (Brierley et al. 1999b). It has been argued that this is indicative of year-to-year variation in krill density. However, there are some instances when multiple surveys have been conducted several weeks apart in the same year that have detected significant differences in krill densities (for example, 2 g m^{-2} wet mass in October 1997 versus 21 g m^{-2} in January 1998; Brierley et al. 1999b). This raises the possibility that apparent inter-annual variability is actually a temporal alias of shorter-term (intra-annual) variability. Most at-sea data available to date on the South Georgia pelagic marine environment are restricted (for logistic reasons) to single, month-long periods in the austral summer. As a consequence, it has not yet been possible to address in detail by direct observation variation in krill density on sub-annual time scales, or to address the potential mechanisms driving any such change. Data from breeding predators ashore at South Georgia have suggested that krill availability can vary significantly throughout the summer breeding season (November-February), but lack of corroborating at-sea data have prevented direct verification of this (Mori and Boyd 2004). Evidence from elsewhere around Antarctica also suggests that local krill densitys can fluctuate substantially within seasons (1994; Siegel et al. 1998).

The possible existence of significant within-year or seasonal variations in krill density have potentially worrying implications for analyses of ecosystem processes at South Georgia that are based on short-term cruise observations, because the timing of the acoustic survey at the island could significantly affect the estimate of krill density for a given ‘year’. Understanding the magnitude, timing and causes of intra-annual variability is thus an essential prerequisite for ecosystem management (Everson 1992a), and to understanding change on an inter-annual scale. Moored instrument arrays can provide simultaneous biological and oceanographic data at the temporal resolution required to resolve short-term variation in krill density and the potential causal mechanism thereof (Brierley et al. 2006; Cochrane et al. 1994). We now have mooring data collected almost continuously between October 2002 and December

2005 that have the potential to provide valuable insight on within-year variation in krill density at South Georgia. This paper details such within-year variation, and examines previously published inter-annual estimates of krill density in light of repeated observations of within-year changes to address the question, "can apparent year-to-year variation in krill density be explained as a simple function of the dates of previous ship-based surveys"?

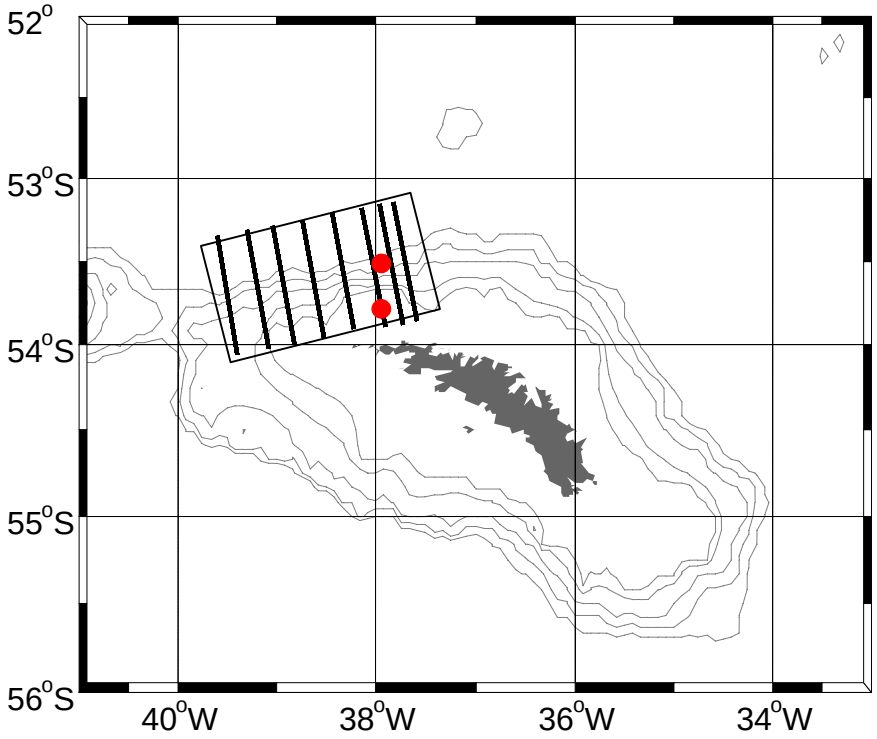

Figure 3.1. Map of South Georgia showing the positions of the moorings and the surrounding bathymetry (300-, 500-, 1000-, 1500- and 2000-m depth contours). The bounds of the British Antarctic Survey western core box region and the 8 standard survey transects are also shown.

3.3. Materials and methods

3.3.1. Mooring Design and Acoustic Sampling

The methods used for the mooring component of this investigation are detailed in Brierley et al. (2006) and so only a summary is given here. Two moorings were deployed at on-shelf and off-shelf locations to the northwest of South Georgia (Figure

3.1). The moorings were first deployed in October 2002 and have remained more-or-less continually in place apart from brief periods (to enable data download, battery replacement and servicing) to the present. The moorings were both equipped with an ASL Environmental 125 kHz Water Column Profiler (WCP), an RDI Workhorse acoustic Doppler current profiler (ADCP) operating at 300 kHz, and a Seabird SBE37 conductivity/temperature/depth logger (CTD). The arrays were positioned in approximately 1300 m and 300 m of water on standard acoustic survey transects (Figure 3.1), and each mooring was engineered so that the instrument package floated at approximately 200 m below the sea surface with the acoustic devices orientated to sample vertically upwards. The ADCPs were configured to collect data in 8 m depth-bins and to ping 7 times within a 4 min ensemble interval. The WCPs were configured to collect data in 0.5 m bins, with a sampling rate of 1 ping every 2 min. Each WCP was calibrated with reference to echo intensities recorded from a standard target during a calibration exercise conducted in Stromness Bay, South Georgia.

3.3.2. Mooring Data Analysis

Mean volume backscatter (S_v dB re 1 m^{-1}) was determined from the WCPs and ADCPs using forms of the SONAR equations presented by Brierley et al. (2006) and Deines (1999) respectively. Both acoustic data streams were processed in SonarData Echoview software. The echograms were first scrutinized for regions of bad data (e.g. near-surface dead zones, 'blank after transmit' and periods of interference). TVG-amplified background noise was then removed according to Watkins and Brierley (1996), and the WCP data were re-sampled (averaged in the linear domain) onto a depth/time grid corresponding to the sampling resolution of the ADCP (8 m × 4 min), enabling frequency differences from equivalent time periods to be determined.

Echoes arising from krill were identified on the basis of the theoretical difference in echo intensity at the operating frequencies of the ADCP and the WCP (S_v 300 kHz- S_v 125 kHz between -14 dB and +14 dB; Brierley et al. 2006). Both the WCPs, however, failed on a number of occasions throughout the time-series (Table 3.1), and an alternative approach was devised to infer krill-related backscatter from single-frequency ADCP data as follows. Firstly, a regression analysis was conducted to

investigate the relationship between ADCP backscatter (30-minute Nautical Area Scattering Coefficient values; NASC) filtered using the dual frequency technique (i.e. data containing identified krill echoes only) and unfiltered ADCP backscatter (i.e. echoes from all targets). The analysis showed that filtered backscatter arising from krill could be inferred using the equation:

$$\text{ADCP NASC}_{\text{filtered}} = 0.86\ \text{ADCP NASC}_{\text{unfiltered}} - 95.97\ (r^2\ 0.92,\ P<0.0001)$$

(i.e. approximately 86% of targets detected were attributable to krill). Secondly, ADCP-derived S_v data were integrated to give unfiltered NASC values at 30-minute intervals. No thresholds were applied to the data prior to echo integration. Finally, all unfiltered NASC values were scaled using the equation above, and values below a threshold of $111 m^2\ nmi^{-2}$ (equivalent to a mean S_v of -78 dB over the mean sampled water column, ~192 m) were removed from the regression-corrected data, so that negative values were not included in the krill density calculation.

3.3.3. Target Strength (TS) and Krill Length-frequency Estimation

The Demer and Conti (2005) stochastic distorted-wave Born approximation (SDWBA) model was used to determine 125 kHz and 300 kHz ventral aspect TS (dB kg^{-1}) for krill with the length-frequency distributions apparent during each mooring deployment period (Table 3.2). Representative krill length-frequency distributions for each time period were determined from length-frequency data obtained from diet samples of Antarctic fur seals and Macaroni penguins that breed ashore at Bird Island and forage in the vicinity of the moorings (Reid and Brierley 2001).

3.3.4. 'Virtual' Survey Transects

ADCP velocity measurements were used to scale time-based acoustic observations of krill over the moorings to area-based density estimates following Brierley et al. (2006). The north and east velocity components for bin 14 (100-108 m depth) were

Table 3.1. Deployment details of the moored instrument arrays. The amount of data collected by each moored instrument and the depth range sampled effectively by the acoustic devices are also shown (✓= complete data stream obtained from instrument, ×= no data obtained, ✓* = data obtained between 20/11/2005 and 20/12/2005).

Deployment	Deployment dates	Approx. water depth (m)	On-shelf mooring depth (m)	Depth range sampled (m)	On-shelf WCP data	On-shelf ADCP data	On-shelf CTD data	Approx. water depth (m)	Off-shelf mooring depth (m)	Depth range sampled (m)	Off-shelf WCP data	Off-shelf ADCP data	Off-shelf CTD data
1	14/10/02-12/02/03	300	196	30-182	×	✓	✓	1300	203	20-189	×	✓	✓
2	19/02/03-28/04/03	300	198	32-184	×	✓	✓	no deployment due to icebergs on site					
3	29/04/03-12/11/03	309	190	32-176	×	✓	✓	1336	208	na	×	×	×
4	12/11/03-13/01/04	310	200	34-186	×	✓	✓	1334	227	21-213	×	✓	✓
5	14/01/04-24/03/04	300	198	32-184	×	✓	✓	1300	226	20-212	×	✓	✓
6	26/03/04-20/11/04	320	199	33-185	×	✓	✓	not deployed off-shelf to avoid fishing fleet					
7	20/11/04-10/01/05	319	197	na	×	×	✓	1300	226	20-210	✓*	✓	✓
8	11/01/05-03/04/05	320	201	35-187	✓	✓	✓	1300	223	17-209	✓	✓	✓
9	04/04/05-29/12/05	300	180	30-166	×	✓	✓	not deployed off-shelf to avoid fishing fleet					

used to construct progressive vector plots (PVPs), which provide a Lagrangian display of Eulerian measurements and can be considered analogous to the cruise track of a research vessel. Each point along the PVPs was transformed to equivalent latitude and longitude coordinates relative to the position of the moorings (using the Geographic Calculator v. 3.09, a Universal Transverse Mercator projection and zone 24 S / 42ºW to 36 ºW), and these data were loaded into Echoview as if they were a survey ship's GPS track data. The latitude and longitude data were then linked by time to the acoustic backscatter data to give a virtual position for each observation.

Table 3.2. Krill lengths and ventral aspect target strength at 300 kHz (ADCP) and 125 kHz (WCP). Values were calculated from predator-derived length-frequency data obtained during each mooring deployment period.

Mooring deployment	Dates of predator diet sampling	Mean Krill length (mm) (=*n*)	Mean TS 300 kHz (dB kg^{-1})	Mean TS 125 kHz (dB kg^{-1})
1	09/10/02-19/02/03	50.5 (1511)	-43.59	-44.82
2	19/02/03-30/04/03	48.4 (754)	-43.57	-44.72
3	30/04/03-12/11/03	45.7 (911)	-42.98	-44.95
4	12/11/03-14/01/04	54.8 (655)	-43.74	-45.04
5	14/01/04-24/03/04	54.0 (733)	-43.63	-44.98
6	24/03/04-24/11/04	61.3 (781)	-43.01	-44.41
7	24/11/04-20/12/04	52.6 (478)	-43.83	-44.92
8	12/01/05-30/04/05	54.5 (779)	-43.84	-45.12
9	30/04/05-12/11/05	46.5 (823)	-42.98	-44.96

3.3.5. Calculation of Krill Density from Mooring Data

Echo integration of echoes identified on the basis of their frequency difference as arising from krill enabled 125 kHz NASC values attributable to krill to be determined at 30-minute intervals throughout the deployment period. WCP and regression-corrected ADCP values were scaled to krill density (g m^{-2}) using the appropriate TS for each instrument, generating time-series of krill density at 30-minute intervals for both the on-shelf and off-shelf mooring. For each daily period (military sunrise + 1 hr to sunset – 1 hr), individual half-hour krill density values were multiplied by the flow distance for that half-hour period: flow distance was calculated using spherical trigonometry from the ADCP-derived GPS position for the start and end of each interval. The daily mean krill density was then determined as [sum(density ×

distance)]/[sum(distance)] following Jolly and Hampton (1990). Longer-term means for multiple day periods were calculated as the mean of days within the period, weighted by the sampling distance for each day: this is equivalent to the Jolly and Hampton (1990) method for calculating strata mean densities from data from several transects. Data from the two arrays were combined during periods in which both on-shelf and off-shelf data were obtained. During such instances, longer-term means were calculated as the mean of the combined number of days within each period, weighted by the combined sampling distance for each day.

3.3.6. Calculation of Krill Density from Ship Data

Standard acoustic surveys were conducted in the western core box (Figure 3.1, Brierley et al. 1997) from RRS *James Clark Ross* during the mooring sampling regime (Table 3.3) such that mooring-based estimates of krill density could be considered in context with possible variability over a wider spatial scale. Data were collected from 8 standard transects (80 km long and c. 10 km apart) using a calibrated EK60 scientific echo sounder operating 38, 120 and 200 kHz transducers. Krill were identified on the basis of the theoretical difference in echo intensity at 38 kHz and 120 kHz (S_v 120 kHz-S_v 38 kHz between 2-16 dB), and echo integration was used to generate 120 kHz NASC values for krill at along-track intervals equivalent to the mean flow distance past the mooring in a half-hour interval (typically 137 m) over the depth ranges sampled by the moored devices at the corresponding time periods (Table 3.1). Data were also partitioned for regions on-shelf (land-ward of the 210 m depth contour) and off-shelf (sea-ward of the 300 m depth contour) such that shipboard estimates of krill density could be determined for a like-for-like comparison with the on-shelf and off-shelf moorings. Dorsal aspect krill target strengths were calculated using predator-derived length-frequency data obtained during each cruise period (Table 3.3). We calculated 120 kHz TS values from the TS-to-krill length relationship given by Demer and Conti (2005) that is a polynomial approximation of the SDWBA model output. Weighted transect and box krill mean densities (and variances) were calculated using the method of Jolly and Hampton (1990).

Table 3.3. Cruise dates, krill length and dorsal aspect target strength at 120 kHz (shipboard EK60). Values were calculated from predator-derived length-frequency data obtained at times coinciding with the ship surveys, except during JR107 where length-frequency data were obtained using a Rectangular Mid-water Trawl (RMT8) net.

Cruise	Cruise dates	Dates of predator diet sampling	Mean krill length (mm) (=*n*)	Mean TS 120 kHz (dB kg^{-1})
JR79	15/10/02-19/10/02	09/10/02-23/10/02	46.3 (150)	-42.98
JR82	13/02/03-16/02/03	05/02/03-19/02/03	50.3 (281)	-43.37
JR107	21/11/04-25/11/04	RMT8 net on 20/11/04	44.2 (157)	-42.76
JR116	06/01/05-10/01/05	06/01/05-10/01/04	57.1 (144)	-44.92
JR121	30/03/05-02/04/05	16/03/05-30/03/05	51.8 (220)	-43.58

3.3.7. Investigation of Temporal Aliasing

Acoustic estimates of krill density collected from the western core box between 1990 and 2005 (Brierley and Goss 1999; Brierley et al. 1999b; Reid et al. 2005; Sushin et al. 2000) were compared to the mooring-derived pattern of within-year variation to assess how much apparent year-to-year variation could be attributed to the survey date. These previously published estimates had been calculated using the krill TS model of Greene et al. (1991) and were thus not directly equivalent to the krill density estimates from this investigation (determined using the SDWBA modelled TS). Existing krill density estimates were therefore rescaled as follows to account for the TS differences. Firstly, the SDWBA model of Demer and Conti (2005) was used to calculate new 120 kHz TSs appropriate for the mean krill lengths observed during each of the previous surveys. Secondly, the dB difference between TS derived from the model of Greene et al. (1991) and TS from the model of Demer and Conti (2005) was determined, and an appropriate scaling factor was calculated to apply to each survey density estimate (scaling factor = $10^{(\text{dB difference}/10)}$). Finally, all previously published krill density estimates were multiplied by the respective scaling factor and, where possible, individual line-transect densities obtained on those surveys were rescaled to enable calculation of the appropriate mean weighted variances following Jolly and Hampton (1990).

3.4. Results

An almost continuous time-series of ADCP data was obtained at the on-shelf location between 14 October 2002 and 29 December 2005 (Table 3.1). However, the off-shelf time-series was interrupted on a number of occasions. The off-shelf mooring was not deployed during February 2003 due to the presence of large icebergs at the site, and no data were obtained between 29 April and 12 November 2003 following the mooring being dragged prematurely to the surface by fishing gear. The mooring was not deployed at the off-shelf location during the subsequent over-winter periods (26 March to 20 November 2004 and 4 March to 29 December 2005) to avoid potential instrument loss by fishing. Furthermore, the reliability of the WCPs was disappointing: both the on-shelf and off-shelf instruments were subject to a number of mechanical and technical faults during each deployment and, despite extensive efforts to improve their performance (including tank-tests), data were only obtained from the two deployment periods 11 January-3 April 2005 and 20 November-20 December 2005.

A distinct pattern of seasonal variation in krill density was evident from the ADCP time-series and this pattern recurred over all 3 seasons (Figure 3.2). Power spectrum analysis showed maximal power at approximately 52 weeks (i.e. annual). In each year, prominent changes in krill density occurred after March and November, dividing the time-series into three distinct summer (December to April 2002/03, 2003/04, and 2004/05) and winter periods (May to November 2003, 2004 and 2005). Peaks in density generally occurred in summer (mean = 89.5 g m^{-2} SD 64.2), with predominantly low krill density apparent throughout the winter (mean = 18.7 g m^{-2} SD 24.3). Shipboard estimates of krill density were not statistically different from those from moored ADCP and WCP data during adjacent time periods (for each cruise, 2-sample t-tests between 8 ship transects and the first 8 days' mooring observations during corresponding time periods, $P>0.05$).

Average seasonal variation in krill density from the 3-year period is shown in Figure 3.3. These mean time-series data were explored using regression analysis. An exponential sinusoidal function with annual cyclicity (i.e. period = 52 weeks) fit the

weekly mean data significantly (P<0.0001). Based on the 3-year ADCP time-series, the density of krill for a given week of the year is given by:

Krill density (g m^{-2}) = exp(3.079 + 1.545cos[0.1208(x – 5.35)]) (r^2 = 0.64, P<0.0001)

where x is the week of the year from 1-52 (1-7 January = week 1).

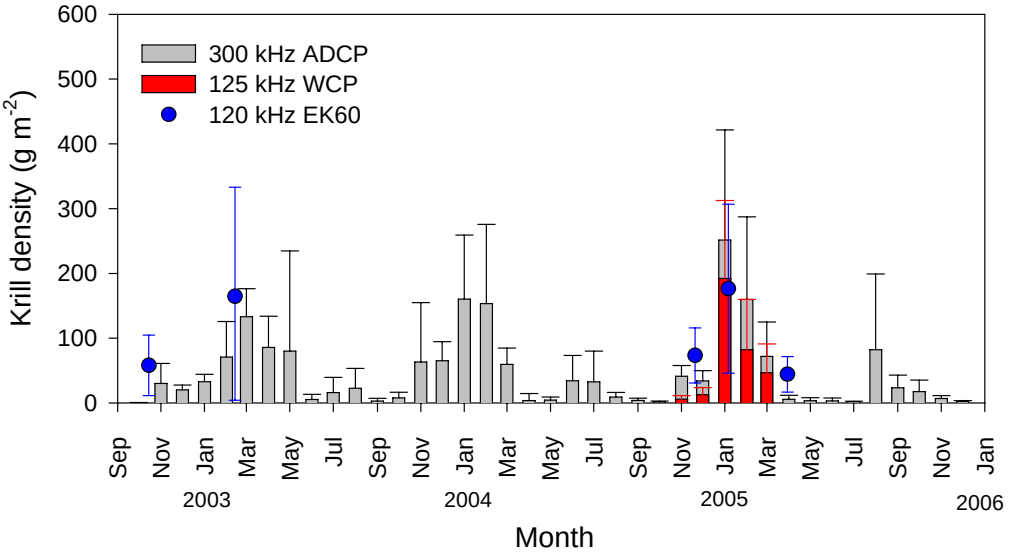

Figure 3.2. Monthly estimates of krill density from the on-shelf and off-shelf moorings during 2002 to 2005. Estimates of krill density in the Western Core Box obtained from standard acoustic surveys are also shown. The error bars are the 95% confidence intervals.

Many (14 from 17) of the published ship-based estimates of krill density in the western core box region between 1990 and 2005 did not differ significantly from the values predicted for the week of survey (for each cruise, Student's t-tests between the multiple ship-transect densities and the corresponding regression-predicted value, P>0.05). However, some survey estimates were significantly different (P<0.01) from the densities expected under the average pattern of within-year variation detected by the moorings. The mid-summer density estimates obtained during 1993/94 (JR06: 17.1 g m^{-2}, CV 15.5%), 1998/99 (ATLD: 29.1 g m^{-2}, CV 26.0%) and 1999/2000 (JR38: 40.3 g m^{-2}, CV 12.3%) were significantly lower than the expected values for the times of year at which the surveys were conducted (Figure 3.3).

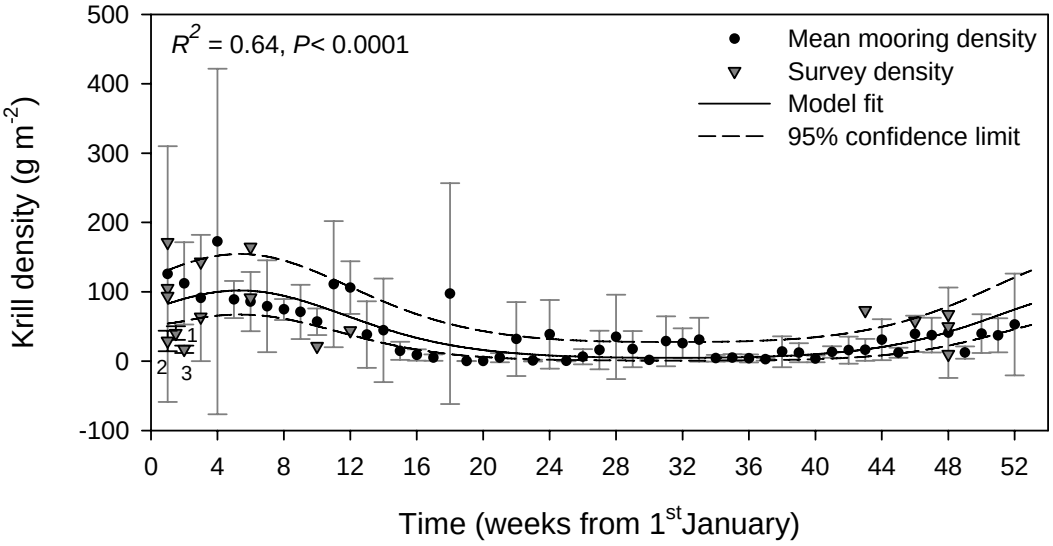

Figure 3.3. Observed variability in krill density at South Georgia by week during 2002 to 2005. The error bars are the ±95% confidence intervals of the observations. Cruise numbers of the outliers are denoted: 1= JR38 (1999/2000), 2= ATLD (1998/99) and 3= JR06 (1993/94).

3.5. Discussion

The time-series of monthly variation in krill density at South Georgia presented here provides insight into the timing and magnitude of variation in krill abundance that has hitherto been hidden from conventional ship-based approaches. Mooring-derived estimates of krill density were not statistically different from the point values obtained from standard ship methods in overlapping or close time periods (± 2weeks), indicating that the moorings provided a representative view of change in krill density at the spatial scale of at least the western core box (80 ×100 km). This is reassuring considering that krill distributions are characteristically patchy around South Georgia (Trathan et al. 2003). The results are also pleasing considering that the time-series of krill abundance were derived largely from single frequency ADCP data. Problems with using an ADCP as a substitute for a calibrated echo sounder, and issues with identifying echoes from target organisms in single-frequency acoustic data without concurrent net samples have been well documented (Brierley et al. 1998a; Cochrane et al. 1994). The ship-board data were collected using a calibrated scientific echo sounder operating at several frequencies, thus enabling robust estimates of krill

density to be calculated via standard protocols that, to a large extent, validated the mooring-derived values that in many instances were calculated without the ability to directly identify krill echoes. The relatively low pelagic species diversity at South Georgia and the swarming behaviour of krill lends this species in this habitat well to study from moorings.

The pattern of seasonal variation observed here was consistent with that reported previously at the Antarctic Peninsula (Lascara et al. 1999) and from limited data from South Georgia (Brierley et al. 2002b; Heywood et al. 1985b) i.e. high in summer and low in winter. The seasonal trend is also consistent with that evident in fisheries data (Taki et al. 2005). Furthermore, our time-series suggests that occasional peaks of high krill density may occur against the predominately low winter signal (e.g. July-August in 2005 Figure 3.2), and these peaks correspond well with marked shifts in the location of the krill fishery from the northeast to the northwest during these times (Taki et al. 2005; Trathan et al. 1998). Thus our results support the notion that shifts in the krill fishery may relate to local availability of krill (Kawaguchi and Nicol 2006).

The moorings detected high within-year variation in krill density, and a sinusoidal regression model with time as the independent variable explained 64% of the weekly variation. Although the precision of the predictive capacity of the mooring-derived model was quite low (relatively large confidence limits at some times of year; Table 3.4), our analyses provide the first quantitative framework to resolve the possible effects of temporal aliasing associated with 'annual' surveys in the western core box region. Comparison of previous acoustic survey estimates with the observed pattern of within-year variation showed that some of the apparent year-to-year variability detected between 1990 and 2005 could be attributed solely to the fact that ship-based sampling had occurred at different times of year. Thus, this variation was not so much inter-annual as a manifestation of expected intra-annual change. Our model is also in line with estimates from other broad-scale krill surveys that covered part of the northwestern region of South Georgia. These include acoustic surveys conducted in November 1982 (11.7 g m^{-2} CV= 9.5%; Murphy et al. 1991) and February 1986 (29.71 g m^{-2} CV = 47.2%; Goss and Grant 1999). Some of the previously reported variation detected by the 'annual' shipboard surveys was however not simply a

temporal alias of short-term, intra-annual variability, but was unusual within the expected framework. There were three instances when the annual survey estimates were substantially lower than those expected given our new knowledge of seasonal variation, and these densities indicated 'poor' krill years. The 1994 (JR06) value, for example, was one of the lowest acoustic estimates reported for *E. superba* at South Georgia. Thus the notion that large between-year fluctuations in krill density occur within the South Georgia pelagic ecosystem is borne out by comparisons with the mooring observations. We expect that, as the time series of mooring data extends, our knowledge of the scale of intra-annual variation will increase, providing an increasingly robust view of the scale of within-year and between-year variation in krill density at South Georgia.

The causes of inter-annual variability in krill density at South Georgia may well be complex, and involve a number of biological and physical interactions operating at various scales throughout the Scotia Sea (Murphy et al. 1998) and possibly beyond. Analysis of physical data from the moorings alongside the biological data should provide increased understanding of intra- and inter-annual change within the South Georgia pelagic ecosystem, and help to elucidate causal mechanisms. Potential mechanisms include intra-annual variation in ocean circulation, seasonal variation in krill migratory behaviour, and variation in krill population processes, such as growth and predation. Initial analyses suggest that the mooring-derived krill density data are not consistent with a pattern of seasonal growth, production and mortality of a resident krill population, but are consistent with the notion of large influxes of krill in early summer, and of a predator-driven reduction between mid- and late-summer. Seasonal changes in aspects of krill behaviour, such as diel vertical migration and swarming, might also be important factors. For example, studies have shown a distinct winter deepening in the vertical distribution of krill across the Scotia Sea, with swarms occurring as deep as 300 m during the day (Gutt and Siegel 1994; Taki et al. 2005). It is therefore possible that the apparent reduced krill densities in the winter might also be a function of individuals residing below the moorings during the daytime hours in which our acoustic observations were made (cf. Enderlein et al. submitted). Such behavioural mechanisms warrant further investigation (Nicol 2006).

Our mooring time-series casts some light on the scale of deviation from the norm that would have to occur before an 'annual' ship survey could detect a 'low' or 'high' krill year. In general terms, this is around ±35 g m^{-2} in summer and ±20 g m^{-2} in winter from the regression model prediction (exact values are shown in Table 3.4). For example, the expected krill density for week 2 (8-15 January) would be 89.9 g m^{-2} based on our model of intra-annual variability (Table 3.4). A ship survey would have to detect a krill density value with an upper 95% confidence limit that is less than 57.8 g m^{-2} during this time, in order for observers to be able to assert that the year in question was one of atypically low krill abundance from the perspective of an acoustic survey. This contrasts markedly with the previous notion that any 'annual' krill density estimate with an upper 95% confidence limit of less than 15 g m^{-2} is indicative of a 'low' krill year (Brierley et al. 1999b). Our results suggest that a krill density estimate could be considerably higher than 15 g m^{-2} but could, depending upon the time of year it was measured, still reflect a period of abnormally low krill density. Furthermore, it is unrealistic to expect 'annual' ship-based surveys to detect, with much sensitivity, subtle variations in krill density from the now-expected within-year pattern. This may explain why efforts to link functional responses (for example, breeding success) of upper-trophic-level species to fluctuations in prey abundance have so far been largely unsuccessful (however, see Reid et al. 2005). We envisage that mooring data will overcome this limitation, leading in the future to better understanding of ecosystem function at South Georgia, and aid with setting Total Allowable Catch (TAC) limits in an ecosystem context. Indeed, a network of moorings throughout the Scotia Sea might ultimately lead to a greatly-improved knowledge of krill throughout the region, and may aid substantially in the management of the resource in this region and beyond.

Month	Week	Mean	+95% CI	-95% CI
Jan	1	82.7	130.9	52.3
	2	89.9	139.9	57.8
	3	95.8	147.0	62.4
	4	99.8	152.0	65.6
Feb	5	101.8	154.3	67.1
	6	101.4	153.9	66.8
	7	98.8	150.8	64.8
	8	94.2	145.1	61.2
Mar	9	87.9	137.3	56.3
	10	80.4	128.0	50.5
	11	72.1	117.7	44.2
	12	63.5	106.9	37.8
Apr	13	55.1	96.1	31.6
	14	47.2	85.8	26.0
	15	40.0	76.3	20.9
	16	33.5	67.6	16.6
	17	28.0	60.0	13.0
May	18	23.2	53.5	10.1
	19	19.3	47.9	7.7
	20	16.0	43.3	5.9
	21	13.4	39.4	4.5
Jun	22	11.2	36.3	3.5
	23	9.6	33.9	2.7
	24	8.2	32.0	2.1
	25	7.2	30.5	1.7
Jul	26	6.3	29.4	1.4
	27	5.7	28.7	1.1
	28	5.3	28.1	1.0
	29	4.9	27.8	0.9
	30	4.7	27.6	0.8
Aug	31	4.6	27.5	0.8
	32	4.7	27.5	0.8
	33	4.8	27.6	0.8
	34	5.0	27.9	0.9
Sep	35	5.4	28.3	1.0
	36	5.9	28.9	1.2
	37	6.5	29.7	1.4
	38	7.4	30.9	1.8
	39	8.6	32.5	2.3
Oct	40	10.0	34.5	2.9
	41	11.8	37.2	3.8
	42	14.1	40.4	4.9
	43	16.9	44.5	6.4
Nov	44	20.3	49.4	8.4
	45	24.5	55.3	10.9
	46	29.5	62.1	14.0
	47	35.3	70.0	17.8
Dec	48	42.0	78.9	22.3
	49	49.4	88.7	27.5
	50	57.5	99.2	33.4
	51	66.0	110.0	39.6
	52	74.5	120.7	46.0

Table 3.4. Predicted mean krill density (g m^{-2}) and ±95% confidence limits for each week of the year. See text for the equation used to calculate the predicted mean values.

3.6. Conclusions

- A regular annual cycle of variation in krill density was detected at South Georgia between 14 October 2002 and 29 December 2005, with krill densities being high during the summer (89.5 g m^{-2} SD 64.2) and low in the winter (18.7 g m^{-2} SD 24.3).

- A sinusoidal regression model with time as the independent variable explained 64% of the observed week-to-week variation in krill density.

- Within this intra-annual framework, 'annual' ship surveys can only be expected to detect 'high' or 'low' krill density events at South Georgia if they deviate from the mean expectation by more than approximately 35 g m^{-2} in summer and 20 g m^{-2} in winter. From the model predictions, therefore, we should not expect functional response analyses to be very instructive within these ranges of krill density.

- The use of moored instruments will provide new insight into the functional responses of upper-trophic-level species to fluctuations in prey abundance at South Georgia, and analyses are ongoing.

- Linking concurrent biological and physical observations from the moorings will enable the hypotheses that variation in krill density at South Georgia is mediated by prevailing oceanic processes, such as changes in the position of the Sub-Antarctic Circumpolar Current Front, to be tested.

4. Intra-annual variability in the density of Antarctic krill (*Euphausia superba*) at South Georgia: scale of change and potential causal mechanisms[3]

4.1. Abstract

Upward-looking acoustic Doppler current profilers (300 kHz) and echosounders (125 kHz) were deployed on moorings on- and off-shelf at South Georgia (54ºS, 37ºW) to measure density of Antarctic krill continuously over c. 3 years between 14 October 2002 and 29 December 2005. This paper describes the seasonal variation in krill density at the two mooring sites, and uses concurrent oceanographic data to explore some potential mechanisms driving the observed change. A distinct seasonal pattern in krill density occurred consistently over all three years. Krill densities were predominantly low in winter (May to November: 19.2 g m^{-2} SD 23.1) and high in summer (December to April: 112.6 g m^{-2} SD 102.6), with substantially lower krill densities off-shelf than on-shelf. Cross-correlation analysis revealed a significant negative correlation between on-shelf water temperature (at 200 m) and on-shelf krill density following a temperature lag of 1-2 months. There was evidence that seasonal variation in krill density off-shelf was linked to seasonal variation in current velocity: during summer 2004 and 2005 off-shelf krill densities were highest when current velocities were lowest. Marked increases in velocity coincided with marked decreases in krill density and abrupt changes in water temperature towards late-season, which might be indicative of advection of krill out of the region, perhaps by a front or eddie, such as the Sub Antarctic Circumpolar Current Front (SACCF). Data from CTDs deployed on elephant seals and Argo floats between January 2004 and November 2005 indicated that the SACCF was possibly in the region during the winter seasons. However, krill densities were low during these periods, and analyses suggest that seasonal variations in krill density were not driven by seasonal oscillations in the position of the SACCF. Other potential mechanisms driving seasonal variation in krill density, such as krill population processes including growth and predation, and seasonal changes in behaviour, were also considered. Our data are not consistent with a pattern of seasonal growth, production and mortality of a resident krill population at South Georgia, but are consistent with the notion of large influxes of krill in early summer, and of a predator-driven reduction between mid- and late-summer. Moorings provide bio-physical data at a high temporal resolution that are important for understanding the mechanisms controlling short-term, ecologically significant intra-annual variability in krill density at South Georgia. These data are prerequisite for the implementation of robust ecosystem-based management strategies.

[3]The work presented in this chapter is currently in review for publication in Limnology and Oceanography as: **Saunders, R.A.,** Boehme, L., Reid, K., Murphy, E.J., Enderlein, P., and Brierley, A.S. submitted. Intra-annual variability in the density of Antarctic krill *(Euphausia superba*) at South Georgia: scale of change and potential causal mechanisms.

4.2. Introduction

The South Georgia region of the Southern Ocean (54ºS, 37ºW) is characterised by high biomass and productivity of phytoplankton that sustains high levels of zooplankton and vertebrate predators (Atkinson et al. 2001). Against this high productivity, inter-annual variability in the distribution and abundance of Antarctic krill (*Euphausia superba)* at the island has been well documented (Brierley et al. 1999b; Heywood et al. 1985a; Priddle et al. 1988). However, the detailed mechanisms that mediate this natural variation are not well understood. Determining the causal processes that underlie variability in krill abundance is an important perquisite for implementation of robust ecosystem-based management strategies at South Georgia. For example, a variety of marine predators at South Georgia are dependent upon krill, and variability in their breeding success is linked to levels of krill abundance (Croxall et al. 1999). The commercial fishery for krill at the island potentially competes with these predators. Understanding the factors that drive variation in the krill stock is therefore important to minimize the potential overlap both spatially and temporally between natural predators and the commercial fishery (Everson 1992a; Nicol and Endo 1999).

Efforts to understand the mechanisms driving natural variability in krill abundance date back to the early decades of the 1900s when the *Discovery* Expeditions were instigated at South Georgia in association with the whaling industry. Early analyses indicated that high levels of biological variability were associated with changes in mean temperature (Harmer 1931; Kemp and Bennett 1932). Increased abundances of krill at the island were later linked to periods of cold sea surface temperatures (Mackintosh 1972), and Marr (1962) suggested that outflow from the Weddell Sea (cold water) was associated with this increase in krill abundance, providing a mechanistic explanation for the observed link between prevailing hydrographic conditions and fluctuating krill abundance at the island (Deacon 1977). Since then, other authors have argued that a large proportion of the observed biological variability is probably driven by variation in the physical environment (Fedoulov et al. 1996; Maslennikov and Solyankin 1988; Priddle et al. 1988). It has also been suggested that variability within the South Georgia ecosystem may be a manifestation of periodic

events or fluctuations operating throughout the Scotia Sea, or indeed throughout the Southern Ocean as a whole, such as the 7-9 yearly circumpolar precession of sea ice, and El-Niño/Southern Oscillation events (Fedoulov et al. 1996; Murphy et al. 1995; Priddle et al. 1988; Sahrhage 1988; Thorpe et al. 2002; Whitehouse et al. 1996).

Krill at South Georgia are not thought to comprise a self-sustaining population (Mackintosh 1972; Marr 1962), although mature and gravid adults are found there (Ward et al. 1990). It has been hypothesised that the krill population at the island is maintained by oceanic transport of individuals from recognised breeding grounds upstream of South Georgia in the vicinity of the Antarctic Peninsula, the South Orkney Islands and the Weddell Sea (Murphy et al. 1998; Watkins et al. 1999b). Clear links between krill abundance at Elephant Island and South Georgia have been established (Brierley et al. 1999a), and variability in krill abundance at one of these breeding grounds (the South Shetland Islands) has been linked to fluctuating recruitment (Siegel and Leob 1995). This fluctuation has been suggested to be related to sea-ice extent and duration, both of which are important for krill reproduction and survival (Leob et al. 1997; Siegel 1988): the environment beneath winter sea-ice apparently provides favourable conditions for the development of larval krill (Daly 1990) and krill feed under ice in summer (Brierley et al. 2002a). If krill at South Georgia originate from these breeding zones, then seasons characterised by high sea-ice cover in the sector could propagate high krill abundance to the island (Siegel and Leob 1995). Brierley et al. (1999a) showed that krill abundance at South Georgia varied in phase and without lag with variation at the Antarctic Peninsula. Reid et al. (1999b) observed almost simultaneous recruitment failures in krill populations at South Georgia and at the Antarctic Peninsula, further indicating large-scale linkages across the Scotia Sea. The variability in krill abundance observed at South Georgia cannot, however, be entirely attributed to krill variability at the Antarctic Peninsula (Murphy et al. 1998). Discrepancy lies in the fact that the amplitude of change at the two locations differs considerably, and that some year classes that are considered strong at the Peninsula can be completely absent at South Georgia. This raises the possibility of additional sources of variability operating in the South Georgia-Scotia Sea ecosystem, such as variability in oceanic circulation, contributing to variation at South Georgia (Hofmann et al. 1998; Murphy et al. 1998; Murphy et al. 2004b; Thorpe et al. 2004). To take the analogy of these fronts acting as a conveyor belt

carrying krill from the Antarctic Peninsula to South Georgia, the conveyor belt must be moving on a trajectory to South Georgia, provide adequate feeding conditions to sustain krill on passage (Hofmann et al. 1998), and be supplied with krill at the Antarctic Peninsula end, for krill to arrive at South Georgia.

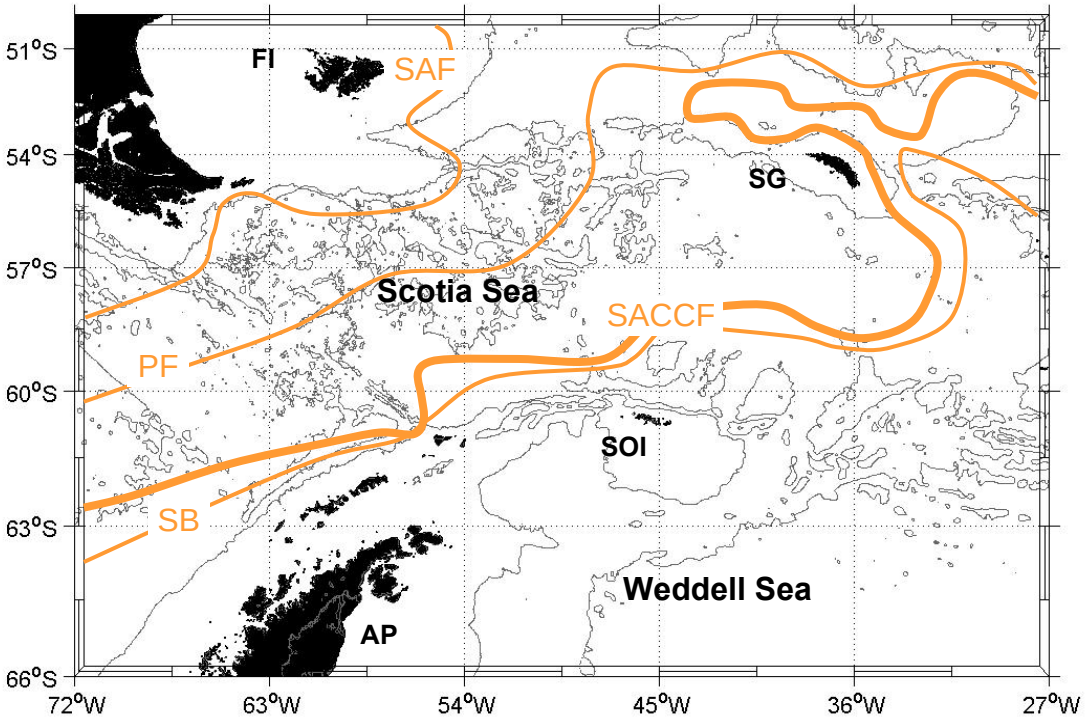

Figure 4.1. Map of the Scotia Sea showing the mean positions of the Sub-Antarctic Front (SAF) following Orsi et al. (1995), the Polar Front (PF) following Moore et al. (1997), the South Antarctic Circumpolar Current Front (SACCF) and the southern boundary of the Antarctic Circumpolar Current (SB), both from Thorpe (2001). Landmasses are AP-Antarctic Peninsula, FI-Falkland Islands, SSI-South Shetland Islands, SOI-South Orkney Islands, and SG-South Georgia.

As krill abundance at South Georgia is probably most strongly influenced by immigration from other sources, oceanic currents have an important role in determining the distribution and availability of krill at the island (Murphy et al. 2004a). South Georgia lies in the path of the Antarctic Circumpolar Current (ACC), which consists of at least 4 current cores embedded in the generally eastward-flowing background flow. These fronts are termed the Sub-Antarctic Front, the Polar Front, the Southern Antarctic Circumpolar Current Front (SACCF) and the southern boundary of the ACC (Figure 4.1). It has been suggested that the SACCF has a crucial role in transport to South Georgia since it passes close to the Antarctic Peninsula and the Southern shelf of South Georgia before retroflecting around the northern shelf of

the island (Hofmann et al. 1998; Murphy et al. 1998; Orsi et al. 1995; Thorpe et al. 2002). The SACCF is oceanographically very dynamic, with intense mesoscale eddy and frontal variability (Nowlin and Klinck 1986). Indeed, Thorpe (2001) demonstrated that the proximity of the SACCF relative to South Georgia could change seasonally. Such variability may have a direct affect on the distribution and transport pathways of krill in the Scotia Sea, resulting in variable krill flux into the South Georgia region (Hofmann et al. 1998; Murphy et al. 1998). It has been hypothesised that the abundance of krill at South Georgia may increase at times when the SACCF impinges more closely, bringing cooler, krill rich waters into the vicinity (Thorpe et al. 2004). Recent observations have recorded a large flux of krill associated with the SACCF north of South Georgia (Murphy et al. 2004b). However, there is presently little empirical data to substantiate clear links between fluctuations in krill abundance and variability in ocean transport systems. This is primarily due to a lack of data.

In order to understand between-year variability in krill abundance and the potential causal mechanisms thereof, it is first necessary to set the context by understanding change on an intra-annual scale. Moorings are able to gather data at a high temporal resolution, and provide new insight into the function of the coupled biological-physical marine ecosystem at South Georgia (Brierley et al. 2006; Saunders et al. in press). There is now increasing empirical evidence from mooring data to suggest that the South Georgia marine ecosystem is characterised by high within-year and seasonal variability in krill density (Saunders et al. in press). Temporal and spatial variability in the density of pelagic marine organisms is typically assumed to be controlled primarily by three factors; ocean circulation, population dynamics and behaviour. In this study, patterns of intra-annual variability in krill density detected by moorings are considered alongside some of the available concurrent oceanographic data to explore possible mechanisms mediating short-term, ecologically significant variation in krill density at South Georgia. Specifically, we examine temperature and velocity time-series for signatures of the SACCF, and see if they are associated with peaks in krill density, thus testing the hypothesis that krill immigration to, and therefore density at, South Georgia is mediated by influx of waters associated with the SACCF. Krill population processes, predation and seasonal variation in krill behaviour are also examined as possible factors mediating intra-annual variation in krill density.

4.3. Materials and methods

4.3.1. Acquisition of mooring data

Upward-looking acoustic Doppler current profilers (300 kHz ADCP) and echosounders (125 kHz Water Column Profiler; hereafter WCP) were deployed on moorings on- and off-shelf to the northwest of South Georgia to measure density of Antarctic krill continuously between 14 October 2002 and 29 December 2005. Each mooring was deployed at approximately 200 m. Concurrent oceanographic data were recorded (at 200 m) using Seabird SBE37 conductivity/temperature/depth loggers (CTD) mounted on the moorings. Full descriptions of the mooring design, deployment details, and instrument configurations are given in Brierley et al. (2006) and Saunders et al. (in press). Each echosounder was calibrated with reference to echo intensities recorded from a standard target during a calibration exercise conducted in Stomness Bay, South Georgia.

4.3.2. Calculation of krill density time-series

Monthly time-series of krill density were calculated from the acoustic data streams following the procedures detailed in Brierley et al. (2006). Those authors provide a full description of the methods so complete details are not repeated here. In brief, echoes from krill were identified on the basis of the theoretical difference in echo intensity at the operating frequencies of the ADCPs and WCPs (S_v 300 kHz-S_v 125 kHz between -14 dB and +14 dB). Echo energy from krill targets at 125 kHz and 300 kHz were integrated at 30-minute intervals throughout the deployment period. Integrated echo intensities were scaled to krill density using target strengths (TS) appropriate for the size distribution of krill in the region. The Demer and Conti (2005) stochastic distorted-wave Born approximation model was used to determine 125 kHz and 300 kHz ventral aspect TS (dB kg^{-1}) for size-frequencies of krill obtained from diet samples from land-based krill predators (Antarctic fur seals and Macaroni penguins) breeding at Bird Island on the western tip of South Georgia (Reid and Brierley 2001). For each daily period (military sunrise +1 hr to military sunset -1 hr), individual half-hour krill density values were multiplied by the corresponding flow

distance for that half-hour period: flow distance was determined from ADCP velocity measurements in the 100-108 m depth bin (approximately the centre of the distributional range for krill swarms at South Georgia in daylight; Taki et al. 2005). The daily mean krill density was then determined as [sum(density x distance)]/[sum(distance)] following Jolly and Hampton (1990). Longer-term means for multiple day periods were calculated as the means of days within the period, weighted by the sampling distance for each day (Jolly and Hampton 1990).

4.3.3. Argo float data and CTD data from elephant seals

To the north and east of South Georgia, the SACCF approaches close to the island (Figure 4.1) carrying water of circumpolar characteristics. The key property indicator of the SACCF is considered to be a temperature of 1.8 ºC at 500 m (Orsi et al. 1995). Argo floats and CTDs deployed on marine mammals can now be used to obtain high-temporal oceanographic data at South Georgia away from infrequent research vessels surveys (Boehme et al. submitted; Boehme and Send 2005; Lydersen et al. 2002). Such methods enable the SACCF to be identified at the appropriate depth interval and provide insight into the timing of the arrival of the SACCF at South Georgia at a similar temporal resolution to our mooring-derived observations of krill. Temperature data collected by Argo floats and CTDs deployed on elephant seals between 1 January 2004 and 1 November 2005 were used to identify the SACCF in proximity to moorings, and substantiate over a broader spatial scale seasonal variations in temperature detected by the moorings. Full descriptions of the methods used to collect and interpolate the data are given in Boehme and Send (2005). In brief, data from both Argo floats and CTDs deployed on elephant seals were interpolated to obtain an optimal estimation of temperature at 500 m and 200 m for every 10-day period throughout the time-series for two grid points. The data were interpolated for a 10×10 nautical mile box, and the grid points were located approximately 5.5 km and 4.2 km from the on-shelf and off-shelf mooring, respectively.

4.4. Results

4.4.1. Krill density and temperature analyses

A distinct pattern of seasonal variation in krill density was detected at the on-shelf site consistently over all 3 years (Figure 4.2a). In each year, on-shelf krill densities were substantially higher in the summer (December to April: mean = 112.6 g m^{-2} SD 102.6) than in the winter (May to November: mean = 19.2 g m^{-2} SD 23.1). Our analyses showed that this seasonal trend in density was not a function of seasonal variation in krill target strength that might be caused by large shifts in krill length-frequency modes throughout the time-series. Analyses also showed that seasonal changes in backscatter intensity due to seasonal variation in temperature and salinity (and hence sound speed and absorption coefficients) did not have an impact on the observed krill density time-series.

The on-shelf time series was examined in relation to the monthly mean water temperature observed concurrently at 200 m (Figure 4.2a). The seasonal variation in krill density varied almost out of phase with the seasonal temperature regime. Higher krill densities occurred generally around periods of low temperature (~0.75 ºC), and low densities occurred at times when temperatures were high (~1.5 ºC). A 1 month cross-correlation window was used to asses lead/lag patterns of correlation between the two variables (Figure 4.3). The most significant negative correlation occurred following a temperature lag of 2 months (r = -0.40, P<0.05) (a significant negative correlation also occurred after a temperature lag of just 1 month; r = -0.35, P<0.05), and the most significant positive correlation following a temperature lead of 4 months (r = 0.63, P<0.001).

The off-shelf time series was broken on a number of occasions due to technical and logistic factors, and no data were obtained during winter (Figure 4.2b). The data available indicate that krill densities were substantially lower off-shelf in summer than on-shelf (for example, 41.6 g m^{-2} ± 22.7 95% C.I. cf. 425.9 g m^{-2} ± 286.4 95% C.I. in January 2005). Although seasonal trends in krill density were more difficult to elucidate at the off-shelf site due to a lack of winter data, the pattern of variation

throughout the summer seasons was consistent with that detected on-shelf, suggesting that the same seasonal pattern in variation might have occurred off-shelf. The available temperature data also followed a very similar pattern to that observed on-shelf during the times in which data were obtained. This suggests a possible association between low temperature and high krill density at the off-shelf site similar to that detected on-shelf.

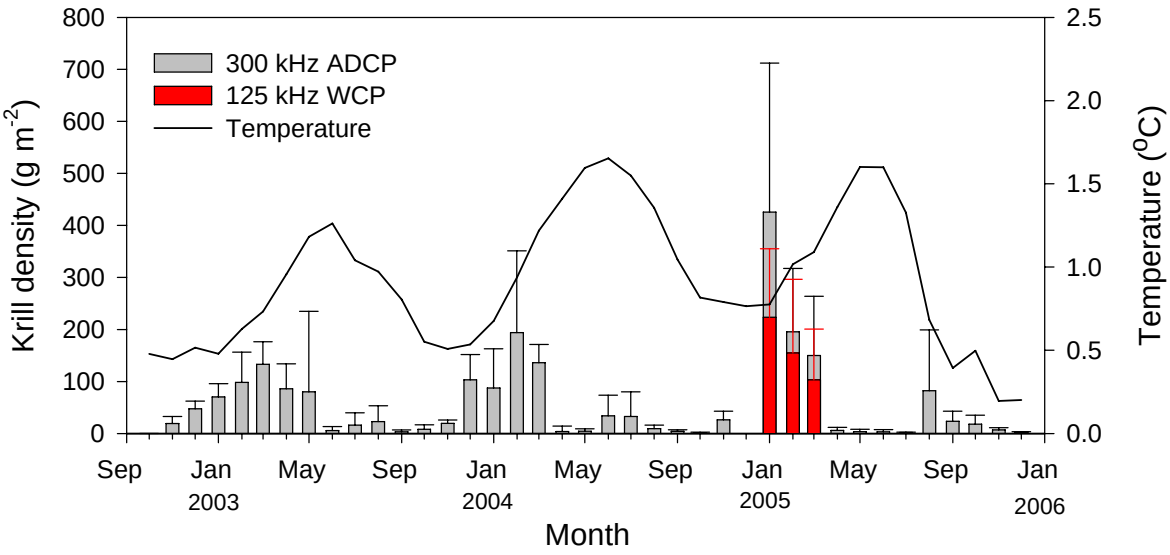

Figure 4.2a. Monthly estimates of krill density from the on-shelf mooring during 2002 to 2005. The error bars are the 95% confidence intervals. The month mean temperature at 200 m is also shown.

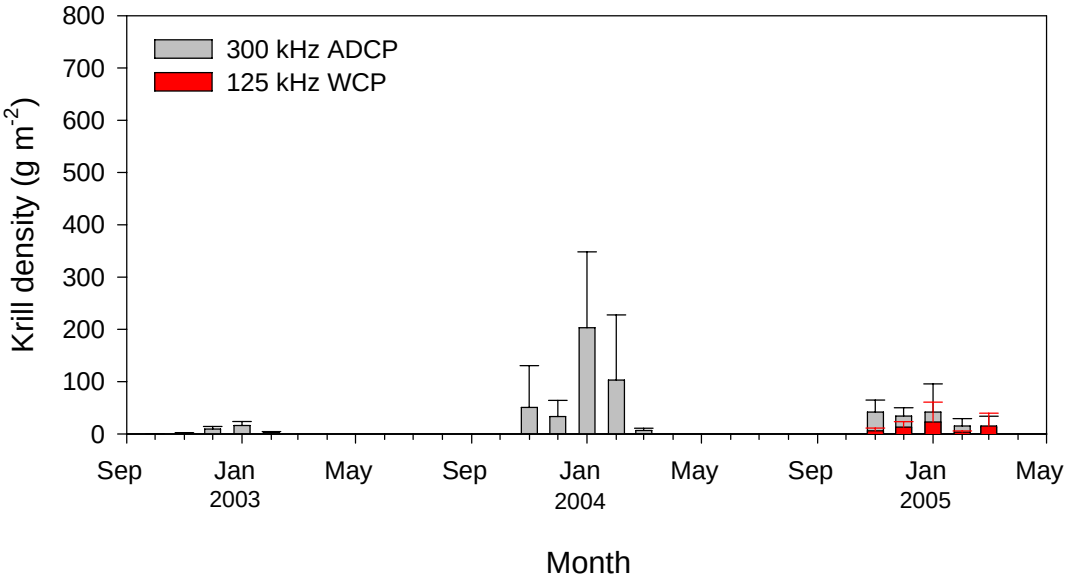

Figure 4.2b. Monthly estimates of krill density from the off-shelf mooring during 2002 to 2005. The error bars are the 95% confidence intervals. No data were obtained between March-October 2003 and April-October 2004.

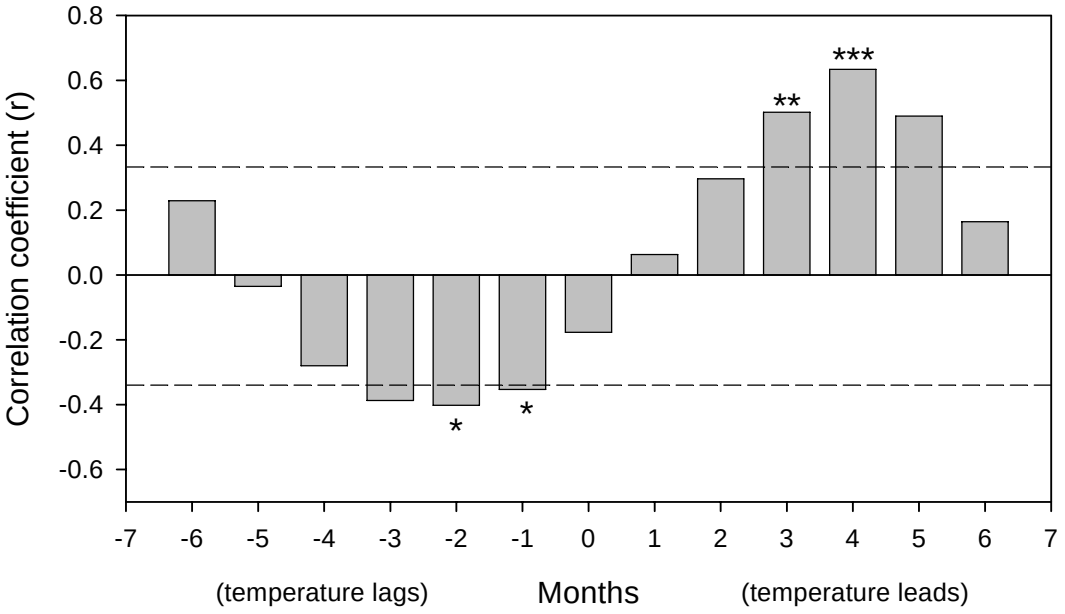

Figure 4.3. Strength of correlation between on-shelf water temperature at 200 m and on-shelf krill density, with temperature leading (positive) or lagging (negative) by up to 6 months. The dotted lines are the ±95 % confidence intervals and the levels of significance are denoted * (P<0.05), ** (P<0.01) and *** (P<0.001).

Saunders et al. (in press) showed that the mooring-derived estimates of krill density in this time-series were representative of those observed at higher spatial scale (ca. 80× 100 km) from conventional shipboard surveys. Here, temperature data from the moorings were additionally compared to those obtained at 200 m via CTDs deployed on Argo floats and elephant seals between 2004 and 2005 to validate the temperature results over a broader spatial scale. Data from these platforms are shown in Figures 4.4a and 4.4b for the regions closest to the on- and off- shelf mooring, respectively. A distinct seasonal pattern in temperature variation was detected between January 2004 and November 2005 that echoed the seasonal pattern detected by the on-shelf mooring (Figure 4.4a). The on-shelf mooring temperature data were highly correlated with the data obtained by the two alternative platforms (r = 0.77, P<0.001). Data obtained in proximity to the off-shelf mooring site also showed a pattern of seasonal variation in temperature similar to that detected by both the on- and off-shelf mooring (Figure 4.4b), and, temperature data from this region were significantly correlated with those obtained by the moorings (r = 0.50, P <0.05). These results suggest that the same

pattern of seasonal variation in temperature occurred on- and off-shelf, and that the mooring data were representative of processes occurring over a wider spatial scale.

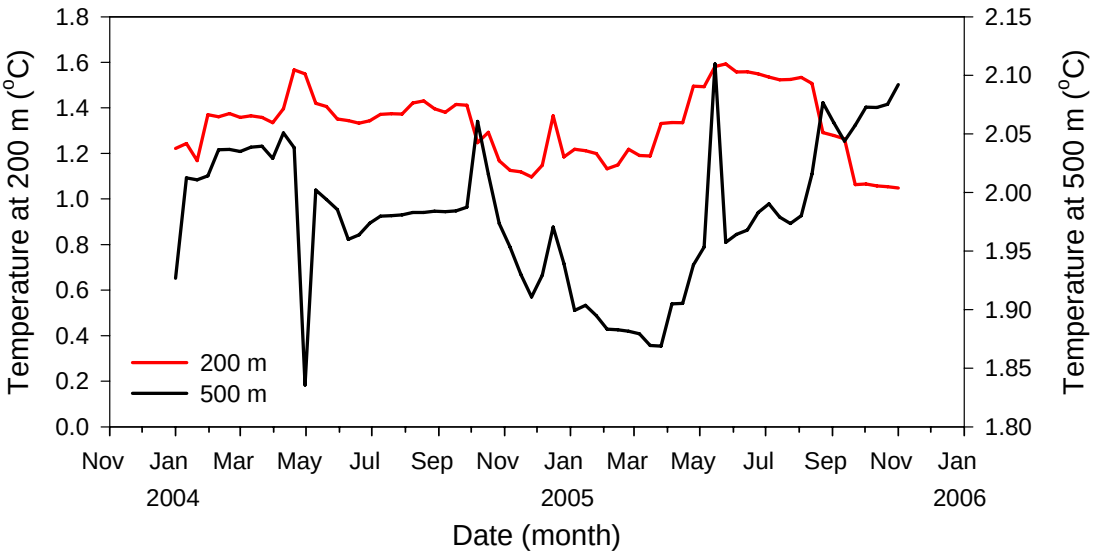

Figure 4.4a. On-shelf time-series of temperature derived by optimal interpolation of Argo float and animal-borne CTD data for a grid point situated approximately 5.5 km from the on-shelf mooring. A property indicator of the SACCF is considered to be water temperatures of around 1.8 ºC at 500 m (Orsi et al. 1995).

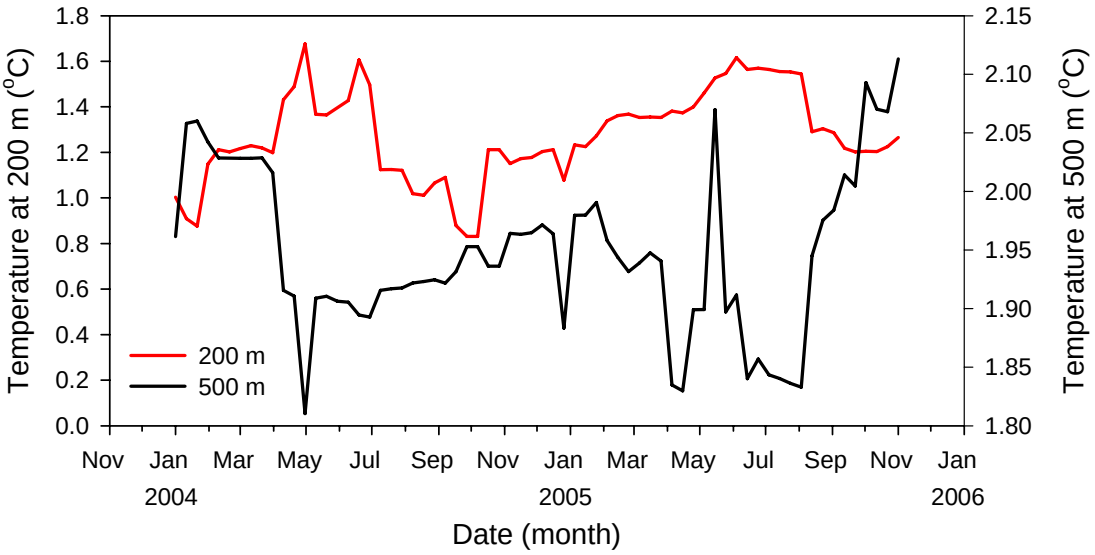

Figure 4.4b. Off-shelf time-series of temperature derived by optimal interpolation of Argo float and animal-borne CTD data for a grid point situated approximately 4.2 km from the on-shelf mooring. A property indicator of the SACCF is considered to be water temperatures of around 1.8 ºC at 500 m (Orsi et al. 1995).

4.4.2. Krill density and position of the SACCF

The SACCF signature is difficult to detect at 200 m (Orsi et al. 1995), and there was little evidence of the SACCF from the mooring data or the Argo float/seal data at this depth. However, data obtained at 500 m by Argo floats and seals foraging in proximity to the moorings provided valuable insight into the possible occurrence of the SACCF during 2004 and 2005 (Figures 4.4a and 4.4b). Based on the SACCF signature of Orsi et al. (1995), the data suggest that the SACCF rarely extended into the region closest to the on-shelf mooring in 2004 (Figure 4.4a). Temperatures were predominantly greater than 1.90 ºC, except during May 2004 when an abrupt decrease in temperature was detected. A temperature signature typical of the SACCF was detected in the region around February to April in 2005 (temperatures around 1.86 ºC), during which time krill densities were decreasing (Figure 4.2a). Peaks in krill density occurred generally at times when temperatures were above the signature of the SACCF (January/February). However, cross-correlation analysis showed no significant correlations (all $P>0.05$) between variation in on-shelf krill density and temperature at 500 m. The SACCF was detected in proximity to the off-shelf mooring site during May-July in 2004 and 2005 (temperatures generally between 1.81-1.89 ºC; Figure 4.4b). Although there were few observations of krill density during these winter periods, the data available off-shelf and on-shelf suggest that krill densities were low during these times (Figures 4.2a and 4.2b). Peaks in krill density appeared to coincide with times when temperatures were well above those characteristic of the SACCF, but there were insufficient krill data for a robust cross-correlation analyses.

4.4.3. Krill density and current velocity

Preliminary analyses of data from the mooring time-series showed that abrupt changes in krill density were associated with abrupt changes in current velocity (Figure 4.5; Brierley et al., 2006). Ward et al. (2002) suggested that variation in current velocity may be linked with mesoscale variation in frontal jets, particularly of those associated with the SACCF. The authors showed that these fronts exhibited higher current velocities (up to 35 cm s^{-1}) than the surrounding water (mean near-surface speeds in the order of 20-28 cm s^{-1}; Hofmann et al., 1998; Ward et al., 2002). ADCP current

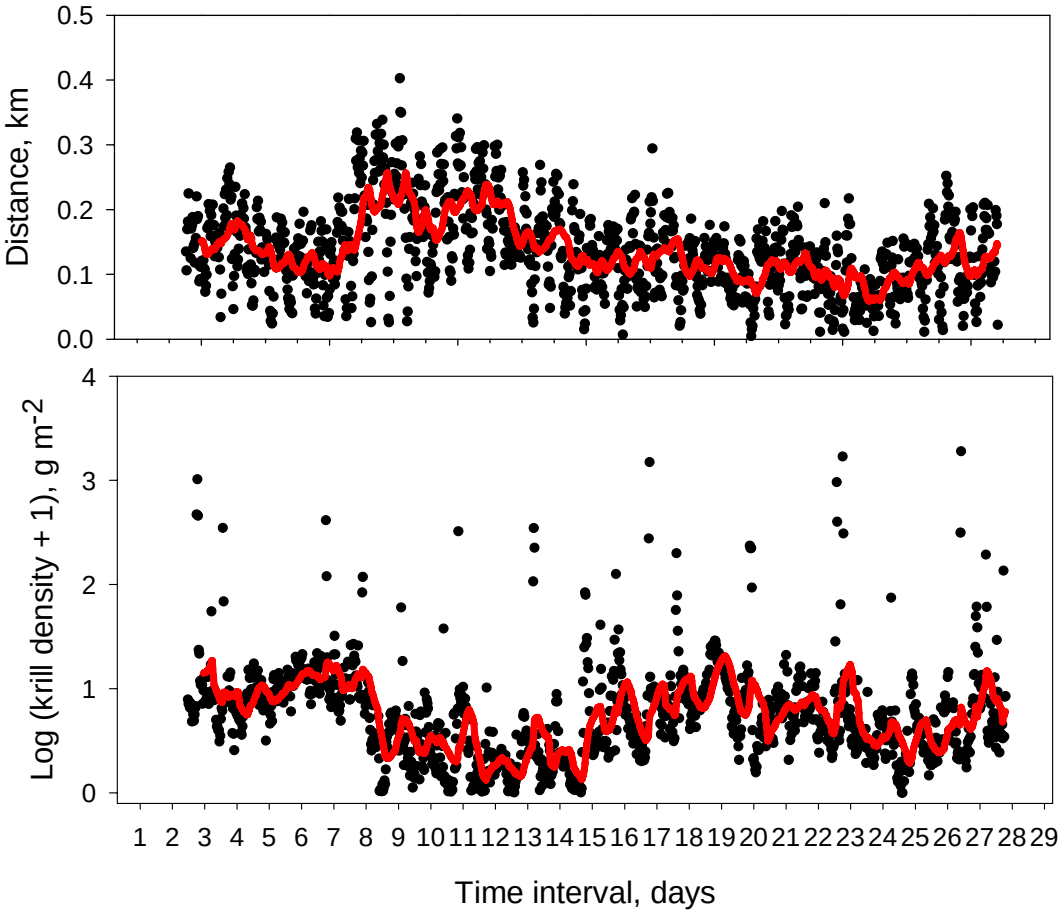

Figure 4.5. Variation in off-shelf krill density in relation to current flow during November 2004 and January 2005. Top: time-series of (log) krill density from the WCP, and 24-point moving average (of the log). Bottom: time-series of current flow at from the ADCP, and a 24-point moving average. Day 1 starts 00:00 24 November 1 2004. These data were taken from (Brierley et al. 2006).

velocity data from the moorings were therefore examined for features indicative of frontal variation (such as the SACCF), and were considered in context with seasonal variation in krill density and temperature. Variations in daily current velocities detected by the on-shelf ADCP are shown in Figure 4.6a. There was no evidence of current variability on-shelf. Also, there was no clear seasonal signal in the on-shelf velocity time-series, and the data did not co-vary with the observed pattern of seasonal variation in krill density or temperature at this site. The data available from the off-shelf mooring showed that daily current velocities there were generally higher than on-shelf (mean: 8.3 cm s^{-1} SD 4.1 off-shelf cf. 5.5 cm s^{-1} SD 1.9 on-shelf; Figure 4.6b). There was some evidence to suggest that krill density at the off-shelf location was higher in waters with a lower velocity and *vice versa*. Comparison of the 30-point

(monthly) running means of the daily velocity and density showed that during January 2004 and 2005 peaks in krill density occurred at times when the current velocity was lowest (moving average ~5 cm s^{-1}; Figure 4.6b). In both these years a marked decrease in krill density was evident between January and April that coincided with a progressive increase in current velocity (moving average from ~5 to10 cm s^{-1}). These changes also corresponded broadly with a sharp decline in temperature at 500 m that was indicative of the SACCF and an increase in temperature at 200 m in both years (Figure 4.4b), suggesting that temperature and velocity were linked. This pattern was not evident during the 2002/03 season as the data series ended on 12 February 2003.

4.5. Discussion

4.5.1. On- and off-shelf variation in krill density

At South Georgia, a distinct and repeating pattern of seasonal variation in krill density was observed during the 3 years of the study. The moorings detected high krill densities in the summer and low densities towards the end of the summer season/winter. This pattern was consistent with that reported at the Antarctic Peninsula (Lascara et al. 1999; Siegel 1988) and from previous, but limited observations at South Georgia (Brierley et al. 2002b). The mooring data also showed that krill densities were predominantly higher on-shelf than off-shelf, consistent with previous observations both from South Georgia (Murphy et al. 1991; Trathan et al. 2003) and other regions of the Scotia Sea (Everson and Goss 1991). How and why krill aggregate on-shelf and along shelf-break areas remains unclear, although it has been suggested that behavioural responses to local bathymetry may be important. For example, it has been suggested that reproductive behavioural responses to bathymetry at the Antarctic Peninsula may explain spatial patterns in krill abundance, size, and maturity segregation (Lascara et al. 1999; Siegel 1988). Siegel (1988) and Lascara et al. (1999) observed a distinct spatial segregation of development stages during summer, whereby juveniles were found inhabiting the coastal waters of the Peninsula and spawning adults were positioned in oceanic regions further offshore in proximity to the shelf-break. This spatial succession was thought to be a behavioural

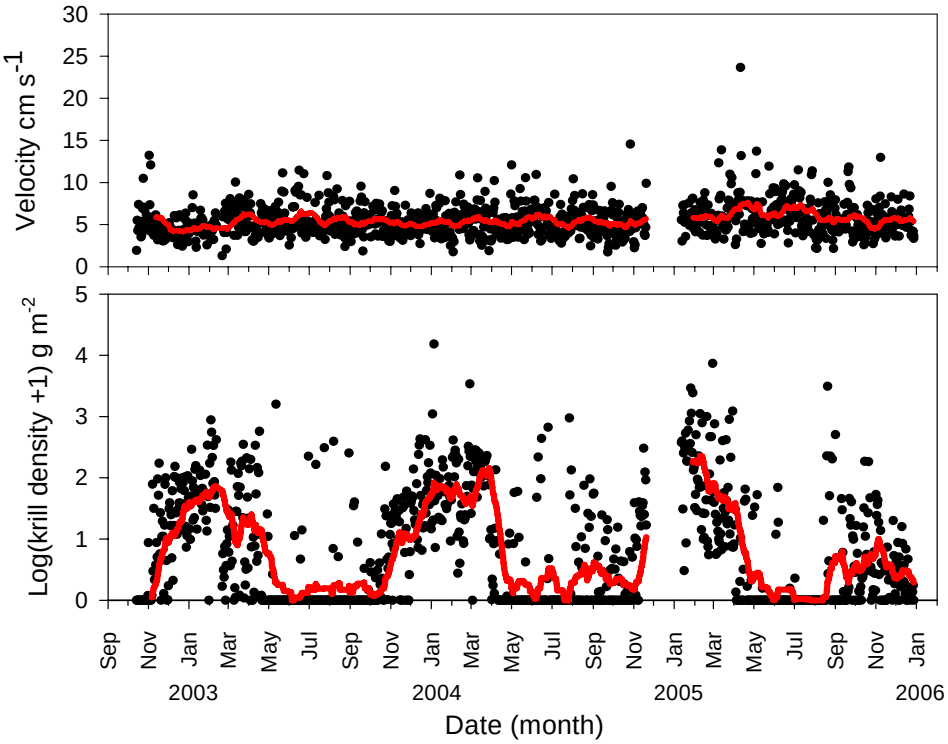

Figure 4.6a. Variation in on-shelf krill density in relation to current velocity. Top: daily current velocity at 100-108 m, and a 30-point moving average. Bottom: daily estimates of krill density from the on-shelf ADCP, and a 30-point moving average (of the log).

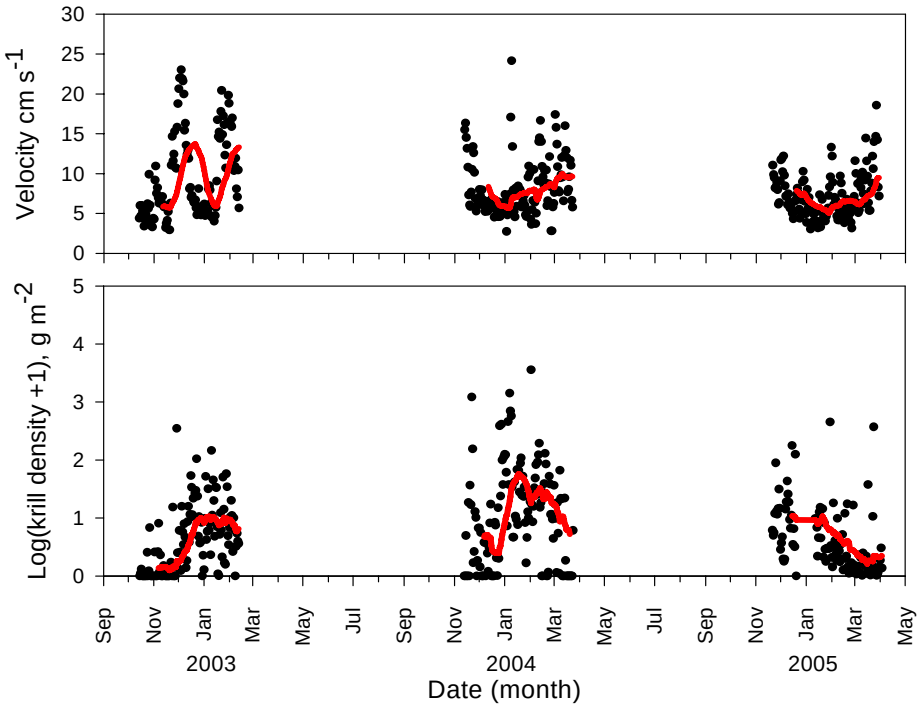

Figure 4.6b. Variation in off-shelf krill density in relation to current velocity. Top: daily current velocity at ~100-108 m, and a 30-point moving average. Bottom: daily estimates of krill density from the off-shelf ADCP, and a 30-point moving average (of the log).

mechanism to maintain high stock densities by minimizing intra-specific competition and parental cannibalism through active offshore/onshore migration of adults (see conceptual model of Siegel, 2000).

Other interactions with bathymetry are also possible. For example, it has been suggested that enhanced primary productivity in regions of upwelling may be an important factor in krill distribution (Everson 1976). In contrast, it is possible that elevated abundances of krill on the South Georgian shelf occur as a result of krill behavioural responses to on/off-shelf water velocity gradients (Trathan et al. 2003; Witek et al. 1988). Witek et al. (1988) suggested that behavioural reactions to water velocity gradients tend to concentrate krill in quiescent areas to the side of strong flow fields. Such low-energy areas close to upwelling systems are generally known to be regions of high plankton abundance, possibly as a function of more productive, stable water conditions (Atkinson et al. 2001). These conditions are typical along the shelf-break at South Georgia. Regions of upwelling occur along the shelf-break, and our results showed that water velocity off-shelf was generally faster than over the shelf (cf. Brandon et al. 2000). Thus, movement of krill onto the shelf from the off-shelf regions (as a function of behavioural responses) could explain the differences in krill abundance at the two mooring sites. The difference in velocity between the sites might also be a function of on-shelf retention mechanisms that cause krill to concentrate in the region because, for example, krill-rich currents, such as the SACCF, pass close to the island from areas upstream. The idea that there are variable small-scale oceanographic processes that determine the local availability of krill by changing retention mechanisms was previously suggested by Murphy et al. (1988) and Brandon et al. (1999). However, it has also been suggested that purely mechanistic factors alone cannot account for such biological accumulation, and that krill behaviour must be an important factor (Hardy 1967; Murphy et al. 2004a; Nicol 2003). Based on experimental and field observations, adult krill appear capable of sustained swimming at speeds between 10 and 15 cm s^{-1} over time scales of hours to days (Hamner 1984; Kils 1981; Marr 1962). We observed on-shelf current velocities that were generally less than 10 cm s^{-1} (mean = 5.5 cm s^{-1} SD 1.9) It seems possible, therefore, that krill would be able to actively maintain their position in the more favourable on-shelf locations as a behavioural response (Trathan et al. 2003), and that both physical and behavioural mechanisms are important in determining local krill

abundance at South Georgia. The cues that mediate krill behavioural responses, such as swarming and active horizontal migration, are not well understood.

4.5.2. Oceanographic mechanisms

Temperature

Oceanic fronts are recognized as important factors determining the distribution and abundance of Antarctic krill (Hofmann et al. 1998; Murphy et al. 1998; Thorpe et al. 2002), and associations between low water temperature and the occurrence of high krill abundance at South Georgia has been hypothesised widely (Deacon 1977; Mackintosh 1972; Marr 1962; Murphy et al. 1998). In particular, mesoscale variability in the SACCF has been highlighted as an important feature in the transport of krill to South Georgia. For example, Hofmann et al. (1998) emphasized the importance of the SACCF in the transport of krill, and concluded that the southern portion of the ACC was the primary vehicle for krill flux from the Antarctic Peninsula region to South Georgia. Our analyses revealed a significant negative correlation between temperature (at 200 m) and high krill density following a temperature lead of 1-2 months, suggesting further that low water temperatures at South Georgia are indicative of water masses that are, or will become, krill rich. Analyses of krill acoustic survey data and oceanographic data together using generalized additive models have also revealed a significant negative relationship between krill biomass and temperature at locations around the island (Trathan et al. 2003). The results presented here are consistent with this previous investigation, and provide evidence for the first time that seasonal fluctuations in krill density in the upper 200 m are possibly linked to within-year variability of sub-surface water temperature. However, a wide range of factors may influence krill density; therefore a simple linear relationship between temperature and krill density is unlikely to exist (Brierley et al. 1999a).

Associations between the occurrence of high krill density and the occurrence of the SACCF at South Georgia throughout the available time-series were weak. At both the on- and off-shelf site, peaks in krill density were detected generally at times (January-

February) when water temperatures at 500 m were higher than those characteristic of the SACCF, indicating that the front was not in close proximity to the moorings. The results further suggest that the SACCF might have been present in the region to the northwest of South Georgia during the winter seasons (May-July) when mooring-derived observations of krill density were markedly low. Thus there was no evidence of large krill flux with the SACCF, and it appears that the pattern of seasonal variability in krill density at the island was not mediated by simple seasonal oscillations of the SACCF. As mentioned previously, for the SACCF to act as a "krill conveyor belt" for transport to South Georgia from the Antarctic Peninsula, the front must, a) be supplied with krill at the Peninsula end, b) move on a trajectory to South Georgia, and c) provide adequate feeding conditions to sustain krill on passage. The observed association between low krill density and the position of the SACCF at the island might therefore be a function of poor krill recruitment at the recognized breeding grounds upstream of South Georgia, linked possibly to the extent/duration of sea ice in the sector, or due to spatial variability in the position of the SACCF en route to South Georgia (Murphy et al. 1998). Also, high krill mortality due to insufficient food availability across the Scotia Sea might have been a key factor (Hofmann et al. 1998). Further data from regions upstream of South Georgia are required to investigate these possibilities, and analyses are ongoing.

Recent oceanographic studies at South Georgia highlight potential difficulties in establishing robust links between variation in krill abundance and variation in the SACCF in our study region, and these factors should be considered accordingly. For example, studies have now shown that low water temperatures around South Georgia might not necessarily be related to the presence of the SACCF, and that cold anomalies at the island could be due to long-term, large-scale climate variation, such as the El Niño Southern Oscillation (Meredith et al. 2005). Meredith et al. (2005) observed an extreme cold anomaly (in 1998) in the region that was due to the combined effects of the passage of a large-scale ocean anomaly that had its origins upstream in the Pacific Ocean, and strong air/sea interaction. Both of these processes were associated with the strong 1997/98 El Niño event, with the ocean response around South Georgia occurring after a very short temporal lag (a few months). In light of this study, it is possible that one (or both) of the low water temperature anomalies observed at the island during this investigation (around April-July 2004 and

2005; Figure 4.4) might be linked to large-scale climate events occurring throughout the southern hemisphere, rather than the occurrence of the SACCF. Further oceanographic data are required to resolve such processes and analyses are ongoing. There is also new evidence to suggest that the SACCF does not always extend directly into the region to the northwest of South Georgia, as suggest by Orsi et al. (1995), and that the front is often confined more to the east/northeast of the island (Meredith et al. 2005; Meredith et al. 2003). Assuming that the SACCF is the primary transport mechanism for krill to South Georgia from regions upstream, the physical (and biological) mechanisms that transport krill from the SACCF to the more western regions of South Georgia remain unclear during such instances. New studies suggest that there are multiple routes for the SACCF to get to the northwest region of the island (Boehme et al. submitted; Ward et al. submitted). These studies show that the SACCF and other coastal water masses may wrap anticyclonically around South Georgia from the south before retroflecting north of the island. Also, Murphy et al. (2004a) suggested that high intensity eddies occurring around the Northwest Georgia Rise may be important in steering mixed waters containing krill from the SACCF into the western regions of the island (cf. Meredith et al., 2003). Such a transport pathway was demonstrated using drifters (Meredith et al. 2003). However, both circulation and the occurrence of the SACCF in this region are highly variable and complex and further data are required to substantiate such a mechanism.

Current velocity

There was no seasonal pattern detected in the on-shelf current velocity time-series, and there is no evidence that seasonal variations in krill density at the site were mediated by seasonal variations in velocity. Considering that krill are able to maintain swimming speeds of around 10-15 cm s^{-1}(Hamner 1984; Kils 1981; Marr 1962), current velocities at this site were generally too low (mean = 5.5 cm s^{-1} SD 1.9) to displace krill from the region. The data available from the off-shelf mooring, however, suggested that seasonal changes in krill density off-shelf were associated with abrupt changes in the magnitude of current velocities. A pronounced decrease in krill density was observed at the site that coincided with a distinct increase in current velocity at the end of the 2004/05 and 2005/06 summer seasons. During the same time periods there was also a marked change in water temperature at both 200 m and 500

m, with the temperatures recorded at 500 m being indicative of the SACCF. These results support the preliminary findings of Brierley et al. (2006) at the off-shelf site that abrupt changes in krill density are associated with abrupt changes in velocity and temperature, and could be indicative of the passage of a front or eddy over the mooring. Ward et al. (2002) reported the presence of two fronts to the northeast of South Georgia, which they considered to be the two sides of a meander in the SACCF. They suggested that these fronts exhibited higher velocities than the surrounding water, and that the SACCF water was distinctly cooler. They also noted elevated krill abundance within the front. It is possible that the off-shelf mooring detected a temporal manifestation of the changes observed spatially by Ward et al. (2002), and that increased velocities caused resident krill to be displaced from the region either as function of advection or behavioural responses to the higher water velocity, as suggested by Witek et al. (1988).

4.5.3. Population dynamics and growth

Recent studies have shown that krill abundance at South Georgia is driven strongly by population dynamic processes (Murphy et al. 1998; Reid et al. 1999a; Reid et al. 1999b). For example, a direct or indirect adverse effect on recruitment processes at South Georgia, or in the regions supplying krill to South Georgia, could significantly alter the population structure, thereby causing a reduction in krill density in the region. Fluctuations of certain year/size classes in the length-frequency distribution are common occurrences at South Georgia (Mackintosh 1972; Reid and Arnould 1996), and it has been suggested that inter-annual variability in krill abundance at the island could be caused by the failure of a single recruiting year class to arrive from the Antarctic Peninsula (Murphy et al. 1998; Reid et al. 1999b). However, large-scale changes between seasons in estimates of krill density are not consistent with the time scales of recruitment and growth exhibited by *Euphausia superba*, which takes 2-3 years to become sexually mature and lives for 5-7 years (Quetin and Ross 2001). For this reason, population dynamics are not considered to be the predominant driving force behind seasonal changes in krill density (Lascara et al. 1999). Siegel (1988) showed furthermore that seasonal changes in krill biomass could not be attributed to krill growth alone. His data from the Antarctic Peninsula showed that from November

onwards, both krill abundance and biomass increased rapidly, and generally reached a maximum plateau at the end of December. Siegel (1988) attributed this seasonal increase to passive drift or advection of animals into the area rather than krill growth, since numbers of krill in all size groups increased substantially during the same time period. A similar mechanism at South Georgia was suggested by Brierley et al. (2002b).

4.5.4. Predation

The reduction in density during the late-season might be evidence for a depletion of krill by predators throughout the peak of the summer breeding season (Brierley et al. 2002b). It is possible that the majority of the krill that were brought in to the region between the early- and mid-season periods were eaten by this time, and krill abundance remained low throughout the winter until the next influx of krill that commenced after November. To investigate this, the decline in krill density observed at the on-shelf site between January and June was considered alongside some of the published rates of instantaneous mortality (including predation) of krill in the South Georgia-Scotia Sea region. Net krill mortality functions are assumed to be constant and are expressed using the equation:

$$N_t = N_0 e^{-Mt}$$

where N_t is the number of individuals in the population at time t from an initial population N_0, and M is the instantaneous rate of mortality. We converted the monthly time-series of krill density (g m^{-2}) to numbers of individuals (m^{-2}) as follows. Firstly, the mean krill length was calculated for each month using predator-derived length-frequency data, and an equivalent biomass (wet weight per individual, g) for each mean krill length was determined using the allometric equation of Morris et al. (1988). Monthly estimates of krill density were then scaled by each respective estimate of biomass per individual krill to generate a time-series of abundance in numbers of individuals per month. Estimates of the instantaneous rate of natural mortality of krill (*M)* were reviewed by Siegel and Kalinowski (1994), who suggested that a range of values between 0.66 and 0.92 yr^{-1} would be appropriate for krill in the

Scotia Sea. Butterworth et al. (1994) used a value of 0.6 with a range between 0.4 and 1.0 yr^{-1}. However, it has also been suggested that rates could be higher at South Georgia due to the large numbers of krill predators (for example, fur seals and penguins) breeding there, with instantaneous mortality rates of 1.25 yr^{-1} (Murphy and Reid 2001) and 1.9 yr^{-1} (Reid et al. 2002). We used a range of estimates from these studies in our analyses. Each annual mortality rate was converted to M $month^{-1}$ to facilitate comparison with our data.

Average variation in monthly krill abundance from the 3-year period is shown in Figure 4.7. These data were explored using regression analysis to determine the best fit of M to the observations. Based on the 3-year time-series, the abundance of krill for a given month between January and June is given by:

$$\text{Krill abundance x (ind. } m^{-2}) = 150.2e^{-0.28x} \ (r^2 = 0.88, P<0.01)$$

where x is the month of the year from 1-6 (1-31 January = month 1).

Thus, the rate of decline between the mid- and late-season can be estimated using an exponent of 0.28, or M = 0.28 mo^{-1} (M = 3.38 yr^{-1}). At the start of the time-series (January) the monthly mean krill abundance was 103.7 ind. m^{-2} (SD 65.5). Based on this starting value, the rate of decline in krill abundance calculated using instantaneous mortality estimates between 0.03 and 0.16 mo^{-1} (annual rates between 0.4 and 1.9 yr^{-1}) were not high enough to account for the observed decline in krill abundance between the mid- and late-season (Figure 4.7). Statistical analyses (Chi squared tests) showed that there were significant differences (P<0.01) between the observed rate of decline in krill abundance and the expected rate of decline using each published estimate of M. Our analyses suggest that mortality and predation were major factors driving the observed decline in krill abundance between January and June. However, the estimated mortality rate is higher than previously considered indicating that other factors are also likely to be involved.

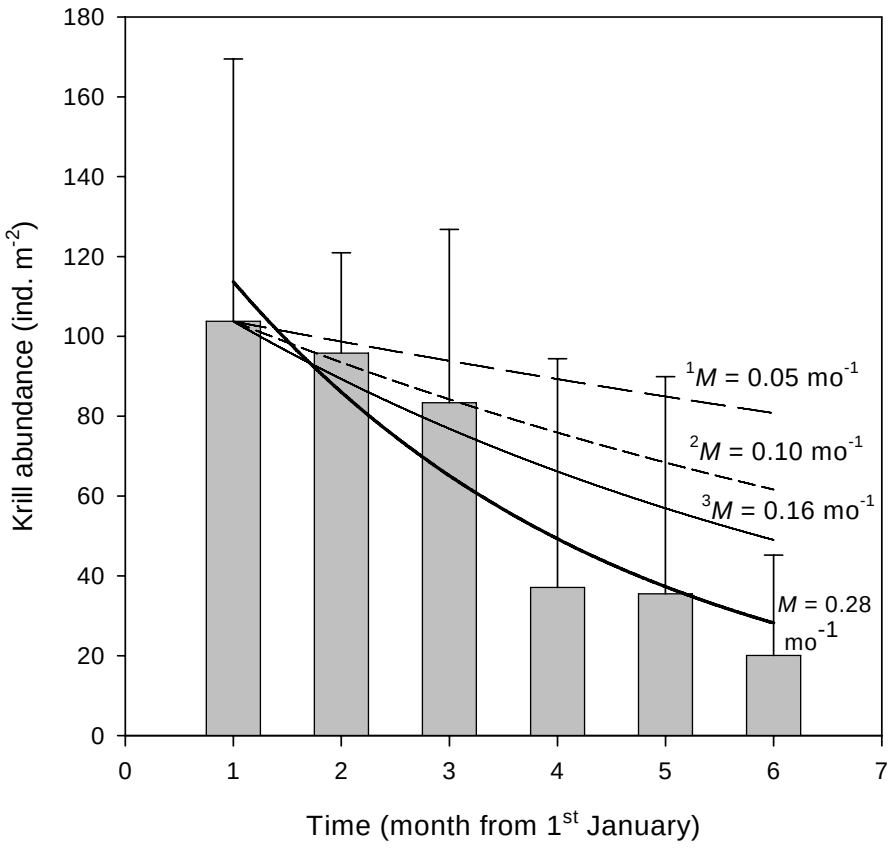

Figure 4.7. Observed decline in krill abundance at the on-shelf mooring site (by month) during 2003 to 2005 in relation to published krill mortality/predation rates for the South Georgia/Scotia Sea region. The heavy black line is the fitted regression line and the error bars are the standard deviation of the observations. Mortality rates (mo^{-1}) are calculated from, 1: M = 0.6 yr^{-1} (Butterworth et al. 1994), 2: M = 1.25 (Murphy and Reid 2001), and 3: M = 1.9 (Reid et al. 2002).

4.5.5. Behavioural processes

The high estimate of mortality may in part be explained by seasonal variation in krill behaviour. Behavioural mechanisms that may influence seasonal variation in abundance include changes in krill swarming patterns and diel vertical migration (DVM) regimes. Foraging behaviour and predator avoidance are often cited as biological factors that influence the formation and maintenance of krill aggregations (Miller and Hampton 1989). The tendency to form aggregations is expected to be highest under conditions of high food availability and high predation pressure (Daly and Macauley 1991). Consequently, spatial and temporal changes in the relative abundance of food and predators should affect swarming behaviour. Studies have

shown that most krill biomass often occurs in small, dense aggregations in the summer, whereas in winter, krill biomass tends to be distributed in larger and more diffuse assemblages (Lascara et al. 1999). Seasonal changes in krill swarming behaviour will directly affect small-scale distributions, which in turn alter the ability to estimate accurately the local abundance of krill according to the capabilities of the sampling equipment. For example, a change in behaviour that favours dispersal rather than swarming would lead to a more uniform spatial distribution, and krill densities may become too low to be detected acoustically using our instruments (minimum detection thresholds for the WCPs and ADCPs are around -85 and -82 dB, respectively).

Vertical migration of krill has been reported from the summer period and occurs generally within the upper 150 m of the water column (Demer and Hewitt 1995; Miller and Hampton 1989), while in more northern latitudes like South Georgia, krill may occur deeper, although still above 200 m (Marr 1962). However, some observations have indicated that during the winter, krill might be benthopelagic or live close to the bottom even at depths of around 400 m (Gutt and Siegel 1994). A winter deepening in the vertical distribution of krill across the Scotia Sea was also observed by Taki et al. (2005) in fishery data, with the highest concentrations occurring as deep as 300 m during the day. It is therefore possible that seasonal changes in vertical migration might be another possible reason to explain the apparent reduced krill densities in the winter, as individuals may have been situated below the moorings during the daytime hours in which our acoustic observations were made. Thus there could have been a large influx of krill associated with the SACCF that arrived close to the moorings in the winter seasons, but our moorings were not deep enough to detect it.

A further possibility is that there could be an active migration process occurring that could have significant effect. Marked seasonal changes in distribution and regional biomass has been recognised around the Antarctic Peninsula, as a result of adult krill migrating on/off shore in summer/winter (Lascara et al. 1999). However, there is currently no evidence to substantiate such a mechanism at South Georgia. These behavioural mechanisms warrant further detailed investigation in order to understand

temporal and spatial variability in krill abundance at South Georgia and throughout the Scotia Sea (Nicol 2003; Siegel 2005).

4.6. Conclusions

In conclusion, a regular annual cycle of variation in krill density was detected on the South Georgian Shelf between 14 October 2002 and 29 December 2005, with krill density being high in the summer and low during the winter. The available data suggest that this pattern also occurred at the off-shelf site, although krill densities were substantially lower than those detected on-shelf. Explanations for the observed pattern of seasonal variation in krill density may be complex, and there is a range of possible factors that could act synergistically to mediate such change. Cross-correlation analysis showed a significant negative correlation between on-shelf temperature at 200 m and on-shelf krill density following a temperature lag of 1-2 months. Limited data from the off-shelf mooring suggested a similar correlation. Data from CTDs deployed on Argo floats and elephant seals provided valuable insight into the timing of the occurrence of the SACCF in proximity to the moorings between 1 January 2004 and 1 November 2005. Peaks in krill density did not coincide with times when the SACCF was detected in proximity to the moorings, and there was no evidence that seasonal variations in krill density were driven by oscillations in the SACCF. There was some evidence to suggest that seasonal variation in krill density at the off-shelf site was linked to changes in current velocity. Krill densities decreased towards the end of the summer season in 2004 and 2005, and this coincided with an increase in current velocity and a reduction in water temperature. However, velocities were slower and more uniform at the on-shelf site, and seasonal variation in krill density appeared not to be mediated by prevailing current velocity. Our data are not consistent with a pattern of seasonal growth, production and mortality of a resident krill population at South Georgia, but are consistent with the notion of large influxes of krill in early summer, and of a predator-driven reduction at between mid- and late-summer. We suggest that seasonal changes in krill behaviour, such as DVM and swarming behaviour might also by important factors, and this warrants further investigation. Our observations did not coincide with seasons of poor krill availability at the island (Brierley et al. 1997).

Moorings provide valuable insight into the coupled biological-physical ecosystem at South Georgia. We envisage that continued use of moorings will provide further data that will be important for understanding, and ultimately predicting, the complex causal mechanisms underlying intra- and inter-annual variability in krill density. Such data are prerequisite for the implementation of robust ecosystem-based management strategies at South Georgia.

5. Regional variation in distribution pattern, population structure and growth rates of *Meganyctiphanes norvegica* and *Thysanoessa longicaudata* in the Irminger Sea, North Atlantic[4]

5.1. Abstract

Euphausiids are a key component of the northern North Atlantic marine ecosystem and *Meganyctiphanes norvegica* and *Thysanoessa longicaudata* are dominant both numerically and in terms of biomass. The Irminger Sea is remote and experiences often-hostile weather conditions. Consequently, few studies have been conducted there, and detailed information on the seasonal distribution, abundance and growth of euphausiids is limited. Here we explore patterns of abundance and spatial and temporal variation in length-frequency distribution in order to determine regional growth rates for both species in the Irminger Basin. Regional composite length-frequency distributions for spring, summer and winter were devised by aggregating discrete net haul data according to the results of a multivariate cluster analysis of length conducted on spring and summer net sample data. Three biologically distinct regions within the Irminger basin were apparent (Central Irminger Sea, Northern Irminger Sea and East of Greenland Shelf). These regions corresponded broadly with distinct physical zones within the basin. Modes in the composite length-frequency distributions were determined by fitting multiple normal distributions, and regional differences in growth were investigated by tracking modes between seasons. The results provide some evidence for regional variability in growth and population dynamics. The population structure and growth of *Meganyctiphanes norvegica* was similar in the open ocean regions of the Northern and Central Irminger Basin, but different in the region around the East Greenland Shelf. There was a distinct absence of larger individuals (+I-group) in the open ocean regions compared to East Greenland Coast region, and growth rates were marginally higher. A similar pattern in population structure was also observed for *Thysanoessa longicaudata*. Variability in growth and abundance are discussed in relation to prevailing environmental characteristics such as temperature and food availability.

[4]The work presented in this chapter was published as: **Saunders, R.A.**, Ingvarsdottir, A., Rasmussen, J., Hay, S.J., and Brierley, A.S. 2007. Regional variation in distribution pattern, population structure and growth rates of *Meganyctiphanes norvegica* and *Thysanoessa longicaudata* in the Irminger Sea, North Atlantic. Progress in Oceanography **27:** 313-342. A copy of this paper is presented in the Appendix.

5.2. Introduction

Euphausiids are a key component in the ecosystem of the sub-Artic and boreal North Atlantic (Mauchline and Fisher 1969; Parsons and Lalli 1988). They graze detritus and phytoplankton and prey upon other small zooplankton such as the copepod *Calanus finmarchicus* (Bamstedt and Karlson 1998). Many of the northern euphausiids are also important constituents of the diet of higher predators, including Baleen whales (*Balaenoptera physalus*), squid (*Loligo forbesi*) and commercially exploited fish species such as Redfish (*Sabastes mentella*) (Gonzalez et al. 2000; Macauley et al. 1995; Vikingsson 1997). Euphausiids have a key role in the transfer of energy through the pelagic food web in the Irminger Sea, which sustains a major international fishery for Redfish (Sigurdsson et al. 2006). The Irminger Sea is, however, remote and often experiences adverse weather. Consequently, zooplankton dynamics, in particular for euphausiids, in the Irminger Sea are poorly understood, especially during the winter.

The Irminger Sea (Figure 5.1) is bounded to the west and north by the continental shelves of Greenland and Iceland, and to the east by the Mid-Atlantic Ridge. Circulation in the surface layers and at depth is counterclockwise around its margin (Lavender et al. 2000). The Irminger Sea can be divided into at least three distinct regions based on the oceanographic properties of the upper 500 m of the water column (Holliday et al. 2006): the Central Irminger basin, which contains an oligotrophic, weakly cyclonic gyre; the region to the west of the crest of the Mid-Atlantic Ridge dominated by the northward flow of the Irminger Current; and the region over the Greenland Shelf slope dominated by the intense southerly flow of the East Greenland current (Lavender et al. 2000). The Irminger Current carries relatively warm, saline water derived from the North Atlantic Current, and retroflects south of the Denmark Strait to join the East Greenland Current. This water mass becomes progressively cooler toward the south as it interacts with colder, fresher water of polar origin from the East Greenland Current, and with the oceanic waters of the Central Irminger Sea.

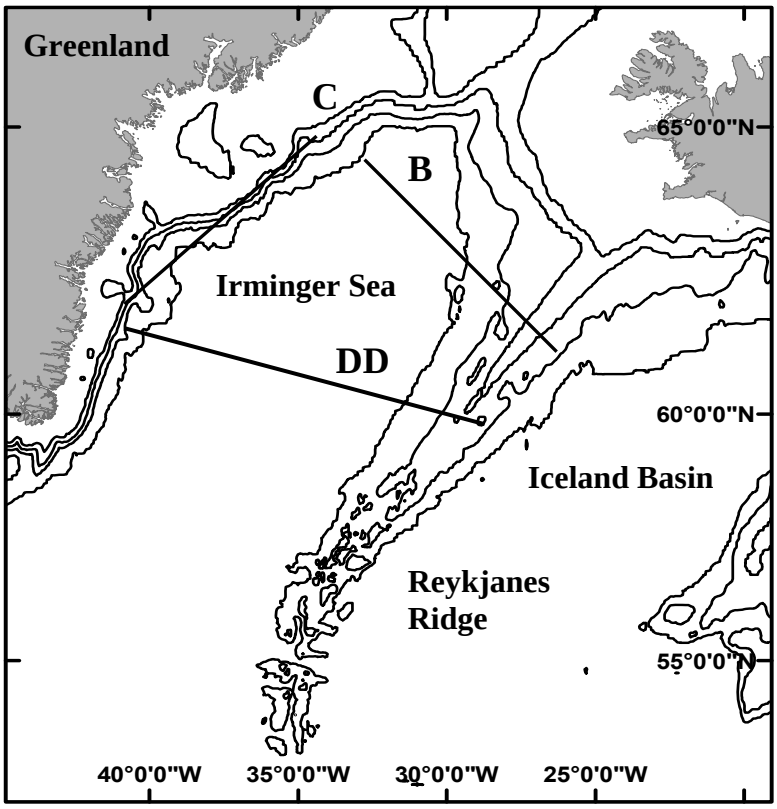

Figure 5.1. Map of the Irminger Basin and the location of the three sampling transects. The 500 m, 1000 m, 1500 m and 2000 m isobaths are also shown.

Several species of euphausiid are found commonly in the North Atlantic (Mauchline and Fisher 1969). In terms of numerical abundance and biomass, the two dominant species are *Meganyctiphanes norvegica* and *Thysanoessa longicaudata* (Einarsson 1945; Lindley 1978). Within-species heterogeneity exists among euphausiids, with populations being adapted locally to very different environments. This is particularly so for *M. norvegica* along European coasts and adjacent seas (Boysen and Buchholz 1984; Labat and Cuzin-Roudy 1999; Lindley 1982; Mauchline 1960) and *T. longicaudata* within the North Atlantic (Dalpadado and Skjoldal 1996; Lindley 1978; Matthews 1973). These adaptations are often manifest as differences in somatic growth and reproductive development, which to a large extent are governed by different underlying trophic (food) and oceanographic (temperature) conditions (Cuzin-Roudy et al. 2004). The Irminger Sea is oceanographically very dynamic (Holliday et al. 2006), and small-scale (within basin), short-term variation in physical environmental conditions may exert a strong influence on the distribution and life cycles of euphausiids. Understanding variation at such small temporal and spatial

scales is central to efforts to understand change in the North Atlantic ecosystem over broader scales (Beaugrand 2003).

The North Atlantic is subject to decadal-scale variations, including the North Atlantic Oscillation (NAO). Recent interest in the possible impacts of climate change on global circulation (Dickson et al. 2002), and the consequences for the ecology of the North Atlantic (Beaugrand 2003; Greene et al. 2003; Richardson and Schoeman 2004), have brought attention to bear on the Irminger Sea. Although a number of investigations have focused on various biological and ecological aspects of euphausiids in the North Atlantic and adjacent seas (Astthorsson and Gislason 1997; Boysen and Buchholz 1984; Einarsson 1945; Falk-Petersen and Hopkins 1981; Jörgensen and Matthews 1975; Lindley 1978; Matthews 1973; Mauchline 1960), information on intra-annual variability in euphausiid growth, distribution of abundance and biomass, and population dynamics within the Irminger Sea has been very limited. Existing net haul data in this region are few and restricted to spring and early summer (Einarsson 1945). Also, these data were collected over a number of years from several different regions within the Basin. Continuous Plankton Recorder (CPR) surveys have provided valuable insight into euphausiid production and population dynamics in the North Atlantic at good temporal resolution (Lindley 1978; Lindley 1982), but these data are restricted to commercial shipping routes mainly outside of the Irminger Basin. CPR data are also limited to the upper 10 m of the water column and the sampling device is size selective (Batten et al. 2003). Many late stage juveniles and adults of euphausiids, such as *M. norvegica*, are too large to be sampled effectively by the CPR. Furthermore, they typically reside at depths below 400 m during daylight hours (Mauchline and Fisher 1969). More comprehensive net haul data are therefore required to understand, and ultimately predict, the possible impacts on euphausiids of long-term, broad-scale environmental change in the Irminger Sea.

In this paper we present data on the seasonal distribution and abundance of euphausiids in the Irminger Sea from net samples collected during spring, summer and winter 2001-2002. Spatial and temporal variation in growth rates and population structure of *M. norvegica* and *T. longicaudata* are investigated using length-frequency analyses. We hypothesize that regional differences in growth and population

dynamics of these two euphausiid species exist for biologically distinct regions within the Irminger Basin, which broadly correspond to distinct physical zones. Observed patterns of variability in euphausiid growth, population structure and abundance are discussed in relation to prevailing environmental characteristics such as temperature and food availability, which are key controls on growth (Waniek and Holliday 2006). Our results provide insight into short-term, small-scale variability in euphausiid biology in the Irminger Sea. These data are needed for effective resource management and robust ecosystem-based management strategies (Deyoung et al. 2004).

5.3. Methods and Materials

5.3.1. Field sampling

Euphausiids were collected as part of the U.K.'s Natural Environment Research Council (NERC) Marine Productivity programme in the Irminger Sea. This included four multi-disciplinary cruises on RRS *Discovery* during winter 2001(cruise D258, 1st November-18th December), spring 2002 (D262, 18th April-27th May), summer 2002 (D264, 25th July-28th August) and early winter 2002 (D264, 6th November-18th December). Sampling was concentrated on three transects within the region (Figure 5.1), which were repeated to varying degrees on the different cruises.

Adult euphausiids were collected using a custom built Dual Methot net. The net system (Methot 1986) incorporates two 1.5 m^2 nets with 1.5 mm mesh that can be opened and closed sequentially at pre-programmed target depths, triggered by a depth sensor on an onboard control logger. The system is deployed with the first net open to a pre-set target depth (e.g. 400 m). This net then closes, and the second net opens and fishes to the desired deployment depth (e.g. 800 m). On the return to the surface, the net system resets to net 1 as it reaches the pre-programmed depth interval such that two discrete strata are sampled. The net deployment is monitored in real time onboard the ship using an acoustic depth sensor system (SCANMAR). A calibrated flow meter is attached to the net frame, and haul durations, net changing times, positions and depths data are determined for each deployment by combining the net system log with the ships navigation log. For this investigation, the net was configured to fish

obliquely from the surface to 800 m, and to provide two depth-stratified samples from 0-400 m and from 400-800 m. Each net was open for approximately 45 minutes and towed at a speed of 1.5- 2.0 knots. The volume filtered by each net was in the order of 15000 m^3. On occasion, technical problems were experienced with the net-closing mechanism, and the sampler failed to collect depth-discrete samples. When such failures occurred (20 failures from 62 deployments), net samples were combined to give an integrated haul between 0-800 m.

Larval stages were sampled with either the ARIES system (Dunn et al. 1993) or with OCEAN Sampler (Dunn et al. 1985; Sameoto et al. 2000). Both samplers were designed to collect a sequential set of discrete plankton net samples delineated by sub-sea pressure intervals during the descent and ascent legs of an oblique towed deployment. The ARIES used a 200 µm aperture mesh filtering net and stored a sequence of samples at intervals corresponding to 50 or 75 m between the sea surface and a maximum of 3000 m depth. The OCEAN sampler was equipped with 7 nets that were opened and closed in sequence on the ascent-leg of each tow from 400 m to the surface, according to a pressure schedule corresponding to 100 m depth intervals between 400 m and 100 m, and 25 m intervals between 100 m and the surface. All nets on the OCEAN sampler were of 95 µm aperture mesh. Both plankton samplers were fitted with calibrated flow meters, and the volume filtered per net sample was on the order of 10-15 m^3 for ARIES and 1-2 m^3 for OCEAN sampler. The 200 µm mesh in the ARIES system retained euphausiid furcilia, nauplii and calyptopis stages, but not eggs. The 95 µm fine net of OCEAN sampler retained all larval stages, but under-sampled the larger furcilia stages due to the smaller volume filtered per sample.

All zooplankton samples were fixed in 4% borax-buffered formaldehyde solution for subsequent taxonomic and morphometric analysis back at the laboratory. Regular CTD casts were conducted on each line-transect during the four research cruises, and chlorophyll *a* concentration was measured from seawater samples collected throughout the water column. These data and associated methodology are detailed in (Holliday et al. 2006) .

5.3.2. Laboratory zooplankton analysis

Euphausiid larvae were identified and enumerated from the OCEAN sampler and ARIES samples using a binocular microscope and a Bogorov tray. All samples were sub-sampled quantitatively using a 5 ml Stempel pipette. The euphausiid larvae were separated into the following stages: (i) nauplii and metanauplii, (ii) calyptopes, (iii) *M. norvegica* furcilia, (iv) *Thysanoessa* furcilia and (v) other euphausiid furcilia. The euphausiid eggs in the samples were only counted, and not separated to species. For this investigation, ARIES data were integrated between 0-800m, and Ocean sampler data were integrated between 0-400 m.

Large samples from the Dual Methot net were sub-divided quantitatively using a Folsom splitter, usually to an aliquot of $1/8^{th}$, and from catches of less than 100 specimens all euphausiids were examined. All euphausiids were identified to species level and total length (front of the eye to the tip of the telson) was measured to the nearest mm for a random sub-sample of 100 individuals from each depth stratum. Sex and maturity status were recorded when possible according to the classifications of Boysen & Buchholz (1984) as adapted from Makarov & Denys (1981). The more generalized maturity classifications of Lindley (1978) were used for the smaller euphausiid species, such as *T. longicaudata*, because the secondary sexual characteristics are less visible. Total dry mass per species per haul was calculated from the total length measurements using the regression provided by Lindley (1978):

$$W = 1.3337\ L^{2.916}$$

where W = dry weight (µg) and L = total length (mm). This equation was based on krill that were measured using standard length 1 (tip of the rostrum to the tip of the telson) as the measurement of total length (Mauchline 1980b). In this investigation we measured total length from the anterior edge of the eye to the tip of the telson (Morris et al. 1988), which could incur some bias when calculating biomass using Lindley's equation. To investigate how our measurements deviated from those produced using standard measurement 1, a regression analysis was conducted on a series of measurements obtained from a random sub-sample (100 individuals per species) of the most common euphausiids collected in the investigation (*M. norvegica*, *T.*

longicaudata, *Thysanopoda acutifrons*, *Nematoscelis megalops*, *Euphausia krohni* and *Thysanoessa inermis*). All measurements were made to the nearest 0.1 mm using a stage micrometer. Considering all 700 specimens:

$$\text{Total length}_{\text{standard 1}}(\text{mm}) = 0.9694x + 0.061 \ (r^2 = 0.999, P<0.0001)$$

where x is total length measured from the anterior edge of the eye to the tip of the telson (mm). Measurements did not deviate significantly from 1:1 (paired 2-sample t-test, $P>0.05$; see Figure 5.2). Thus, there were no major differences between the two total length measurement protocols (Figure 5.2), and the error incurred in our biomass calculations using the equation of Lindley (1978) was negligible.

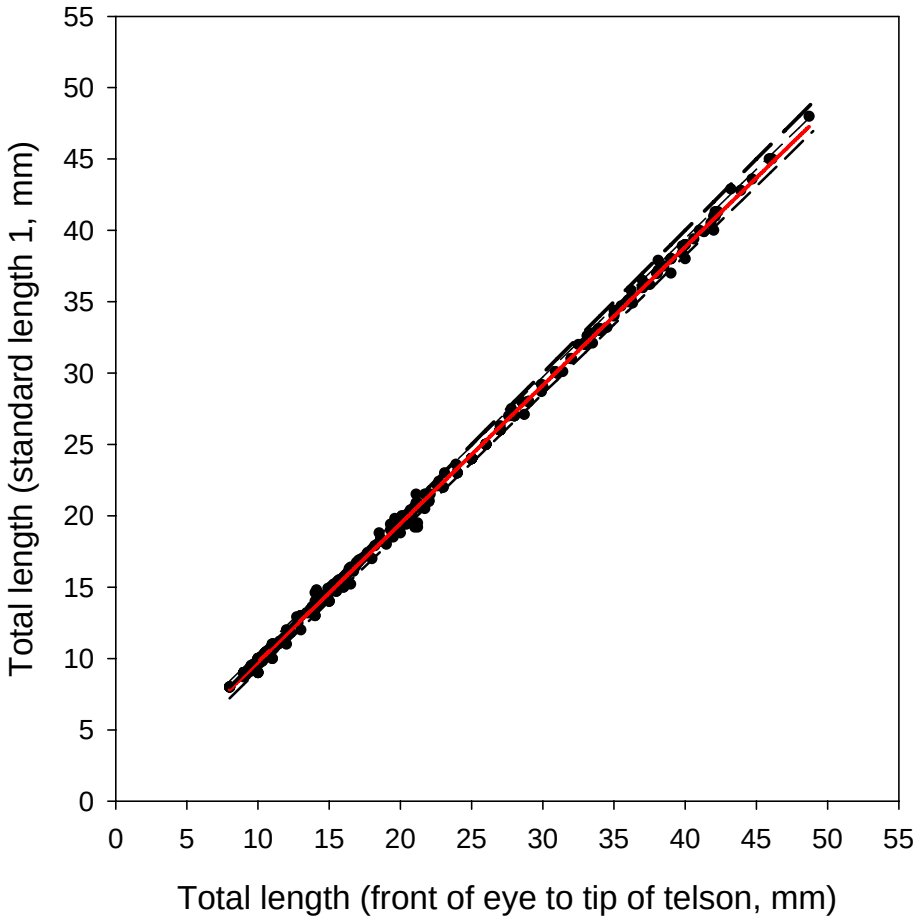

Figure 5.2. Comparison of euphausiid total length measurement protocols. The solid red line is the regression fit, the feint dashed line is the 1:1 and the heavy - dashed lines are the 95% confidence limits of the regression fit.

5.3.3. Effects of diel vertical migrations

Euphausiids exhibit a depth distribution that varies with daylight state. Most euphausiid species perform diel vertical migration (DVM), whereby individuals ascend to the surface layers at dusk and then descend to depth at dawn. A Wilcoxon matched-pairs test was conducted to determine the effect of DVM on the vertical distribution of euphausiid abundance and biomass throughout the sampling regime. The test was performed for all samples, for samples collected during the daytime (sunrise +1hr to sunset) and for samples collected at night (nautical twilight end to nautical twilight start). No separate analyses were performed on the samples obtained during twilight hours as the state of the DVM was unknown and potentially variable between depth strata.

5.3.4. Length-frequency analysis

A series of Kolmogorov-Smirnov tests were conducted on the upper and lower net length-frequency distributions (compiled in 1 mm bins) to investigate possible differences in population structure between the two depth strata. The tests were conducted for each species at stations where there were >60 individuals in both the upper and lower net hauls. For all species, only 5 stations showed significant (P <0.05) differences in length-frequency distribution. It was, therefore, assumed that the individuals obtained below 400 m were from the same population as those situated above 400 m, and length-frequency distributions were combined between depth strata for each euphausiid species. This also facilitated comparisons with stations net hauls that were not depth stratified. Results that showed significant differences came from around the East Greenland Shelf or the northern Reykjanes Ridge where predominantly mixed waters occur.

A hierarchical cluster analysis (Lance and Williams 1967) was used to explore regional patterns of similarity in length-frequency distributions of *M. norvegica* and *T. longicaudata* within the Irminger Basin. Data from spring (D262) and summer (D264) were used for the hierarchical cluster analysis (HCA), because these cruises had the greatest spatial coverage across the Basin. The HCA was conducted by computing a

similarity matrix, containing the relative frequency of each krill length class (each 1 mm bin) at each station and subsequently fusing clusters using the Euclidean distance coefficient (distance = 6) as a measure of similarity (Siegel et al. 2004). The Euclidean distance is effectively the 'straightline' distance (metric) between two clusters after data standardization, and is calculated using Pythagoras's theorem (Waite 2000). Only stations with a minimum of 60 measured specimens were considered in the analysis. Composite length-frequency distributions were then devised for each region by summing the data for each regional cluster. Winter data (D258 and D267) were also aggregated according to these regions.

Modes in the composite length-frequency data were determined by fitting normal distributions using component-fitting software (CMIX; de la Mare, 1994). The method fits a mixed distribution using a maximum likelihood estimator that assumes the length-frequency data have an Aitchison delta distribution (Aitchison 1955). The user must identify the expected number of components within the distribution before initializing the fitting procedure. Based on previous population dynamics investigations, we assumed *a priori* that there were two modes in the *M. norvegica* population, and either one or two components in the *T. longicaudata* population (Einarsson 1945; Lindley 1978). Where the number of cohorts present was not immediately obvious, the best component fit to the observed data was determined using a Chi-squared test. No constraints were placed on the proportions, the mean length or the variance expected within each component when fitting the mixed distributions.

5.3.5. Growth and environmental analyses

Regional growth was determined by tracking modes in the composite length-frequency distributions between seasons (cruises). The difference in modal size was expressed as a rate of growth (mm per day) relative to the number of days that had elapsed between the middle sampling dates of the hauls taken on each transect/region during each cruise. Regional variability in temperature and chlorophyll *a* concentration was then used to model how these underlying environmental conditions affected the growth of *M. norvegica* and *T. longicaudata*. For each season, the

average temperature over 0-40 m, 40-200 m and 200-800 m depth intervals was calculated in each region using data from Holliday et al. (2006). Mean chlorophyll *a* concentration was determined for 0-40 m and 40-200 m. For each species, percentage growth data pooled from each region were plotted against integrals of temperature and chlorophyll *a* concentration (degree days and chlorophyll *a* days). Separate analyses were conducted for each individual cohort, where possible, and for all cohorts collectively. The data were explored using linear regression, and Generalized Linear Models (GLM) following the method of Fox (2002).

5.4. Results

5.4.1. Investigation area and physical environment

The methods and results of the physical oceanographic analyses on the four research cruises are detailed in Holliday et al. (2006). Table 5.1 shows a summary of the physical data presented by those authors for the three distinct regions sampled. In general, temperature, salinity and chlorophyll *a* concentration were low in each region during winter (Nov/Dec). Temperature and salinity increased in spring (Apr/May) and chlorophyll *a* was higher than in the winter. By Jul/Aug 2002 a temperature-dominated pycnocline had developed in each region, and the shallow mixed layers were substantially warmer and also fresher. Post phytoplankton-bloom conditions were evident during this time, and chlorophyll *a* concentrations were similar to those observed in spring (Sanders et al. 2005; Waniek and Holliday 2006).

Throughout the surveys, the Central Irminger Sea region typically had lower temperatures and lower, but highly variable, salinities compared to the other regions, both in the surface waters and at depth (Table 5.1). Physically the Northern Irminger Current zone was very different from the Central Irminger Sea, but in terms of chlorophyll *a* concentration in the surface layers, the two regions were barely distinguishable throughout the four surveys. Both regions had low chlorophyll *a* concentration (0.2-0.8 mg m^{-3}) during each season with the development of only a minor spring bloom apparent from the cruise data. The highest chlorophyll values in the Northern Irminger Current were found over the northern section of the Reykjanes

Ridge (up to 2.0 mg m^{-3}). The physical characteristics in the East Greenland Current Zone are complex, because the East Greenland Current (EGC) carries several different water types. Holliday et al. (2006) separated the zone into two sub-zones: the Polar-Origin EGC Zone and the Atlantic-Origin EGC Zone. The key features of the EGC Polar zone throughout the season were low mean temperatures (3.0-6.1 °C) and salinity (33.95-34.98) and strong near-surface stratification dominated by freshwater. A strong phytoplankton bloom was also observed in the surface waters in the spring season, and chlorophyll *a* concentrations were high (mean 3.2 mg m^{-3}). Relatively few net hauls were conducted in the EGC Polar Zone, as the core of the current lies somewhat inshore of the shelf-break and ice cover prohibited sampling. Temperature and salinity in the EGC Atlantic Zone were consistently lower than in Northern region during spring, summer and winter (Table 5.1). However, chlorophyll *a* concentration was higher (0.1-1.3 mg m^{-3}) in this zone than in either the Central or Northern regions.

Table 5.1. Mean oceanographic conditions in the Central Irminger Sea, Northern Irminger Current Zone and the East Greenland Current (Atlantic) Zone during each cruise/season. These data are summarised from Holliday et al. (2006).

Season	Cruise	Approximate date of sampling	Mean depth of mixed layer (dbar)	Mean potential temper-ature in surface layer (°C)	Mean salinity in surface layer	Mean chlorophyll *a* concentration in surface layer (mg m^{-3})	Potential temperature range below 100 dbar (°C)	Salinity range below 100 dbar
Central Irminger Sea Region								
Winter	D258	14/11/01 - 22/12/01	54	6.5	34.73	0.3	5.0-7.0	34.80-35.10
Spring	D262	3/5/02 - 20/5/02	52	6.9	35.08	0.6	5.0-7.0	34.80-35.10
Summer	D264	1/8/02 - 9/8/02	21	9.7	34.91	0.8	5.0-7.0	34.80-35.10
Winter	D267	no data						
Northern Irminger Current Zone								
Winter	D258	8/12/01	110	7.7	34.99	0.2	7.0-7.5	35.10-35.15
Spring	D262	18/5/02 - 21/5/02	91	7.3	35.13	0.5	7.0-7.5	35.10-35.15
Summer	D264	1/8/02 - 13/08/02	22	10.6	35.05	0.8	7.0-7.5	35.10-35.15
Winter	D267	no data						
East Greenland Current Zone: Atlantic								
Winter	D258	28/11/01 - 14/12/01	237	6.1	34.98	0.1	6.0-7.0	35.00-35.05
Spring	D262	09/05/02 - 17/05/02	19	6.1	35.02	0.9	6.0-7.0	35.00-35.05
Summer	D264	09/08/02 - 22/08/02	22	8.9	34.85	1.3	6.0-7.0	35.00-35.05
Winter	D267	no data						

5.4.2. Vertical distribution of euphausiids

A total of 62 Dual Methot net deployments were conducted in the Irminger Sea and adjacent regions between November 2001 and December 2002, of which 42 were depth-stratified. The results show that for all samples combined (both day and night) euphausiid biomass and density were significantly (P <0.001) higher (over 71 %) in the 0-400 m region of the water column than in the 400-800 m region (Table 5.2). Euphausiid biomass and density were also significantly higher (68 to 74%) in the upper depth stratum during daytime (P <0.01).

Table 5.2. Vertical distribution of euphausiid biomass and abundance, and results of the Wilcoxon signed ranks test to compare differences between the upper and lower depth strata (0-400 m and 400-800 m) during day and night. 15 net samples were collected during hours of twilight: these samples were not analyzed separately as the state of DVM was unknown and potentially variable between strata. 7 of the 9 night nets were taken during winter; therefore the higher densities and biomass observed in the lower nets samples at night reflect a seasonal rather than diurnal deepening (see text).

Comparison	No. nets	% in upper net samples	% in lower net samples	*P*	
Biomass					
All samples	42	70.96	29.04	0.000	***
Day samples	18	68.69	31.31	0.016	**
Night samples	9	40.24	59.76	0.139	ns
Density					
All samples	42	72.70	27.30	0.000	***
Day samples	18	74.50	25.50	0.000	***
Night samples	9	45.60	54.40	0.678	ns

However, both euphausiid density and biomass were not significantly higher in the upper nets than in the lower nets during the night. Around 54 and 59% of the euphausiid biomass and density were located in the lower depth stratum during the night. Of the 9 net samples that were collected during night hours, 7 were obtained during the winter season. Studies on the spatio-temporal variability of epi- and meso-pelagic acoustic backscatter in the Irminger Sea showed that there was a seasonal deepening of the biological scattering layers during the two winter seasons (Anderson et al. 2005). This may explain why euphausiid abundance and biomass were not significantly higher in the upper depth stratum than in the lower stratum during the

night: the apparent diurnal signal we detected in the net samples could have been a manifestation of a seasonal deepening of the vertical distribution. However, there was insufficient winter net sampling and inadequate vertical sampling resolution to explore potential seasonal trends in vertical distribution.

5.4.3. Distribution of abundance and biomass

Several species of euphausiid were encountered regularly in the net samples including *M. norvegica*, *T. longicaudata*, *Thysanopoda acutifrons*, *Nematoscelis megalops*, *Euphausia krohni*, *Thysanoessa inermis*, *Nematobrachion boopis* and *Stylocheiron maximum*. Spatial heterogeneity in euphausiid distribution and abundance within the Irminger Sea was apparent during the study period (Figures 5.3 and 5.4). Winter stations were limited in the region due to unfavourable weather conditions. In general, total euphausiid biomass and density differed for each station and the proportion of each species in the net hauls was not uniform across the Basin. During all seasons, the dominant euphausiid species were *T. longicaudata* and *M. norvegica*. The most numerically abundant species in the region was *T. longicaudata*, with mean densities between 73 and 196 ind. 1000 m^{-3} (Table 5.3).

The species comprised a high proportion of the total euphausiid biomass at most stations during each season (Figure 5.3), and its range of biomass estimates was 72-274 mg 1000 m^{-3}. Abundance of *M. norvegica* was considerably lower than that of *T. longicaudata* (8-194 ind. 1000 m^{-3}) for much of the sampling regime (Table 5.3). However, *M. norvegica* comprised a higher biomass (range: 162-2606 mg 1000 m^{-3}) and formed a substantial percentage of the total euphausiid biomass at the majority of stations, particularly around the East Greenland Coast and the northern Reykjanes Ridge/Icelandic Coast. Stations with the highest overall krill abundance and biomass were generally situated within these two regions during each season.

Thysanopoda acutifrons was present in very low numbers (<4 ind. 1000 m^{-3}) at most of the sampled stations around the Irminger Sea, but it still comprised a relatively high proportion of biomass due to its large body size (Figure 5.3). *Thysanoessa inermis* was confined to a few stations around the E. Greenland Shelf and the Iceland Shelf.

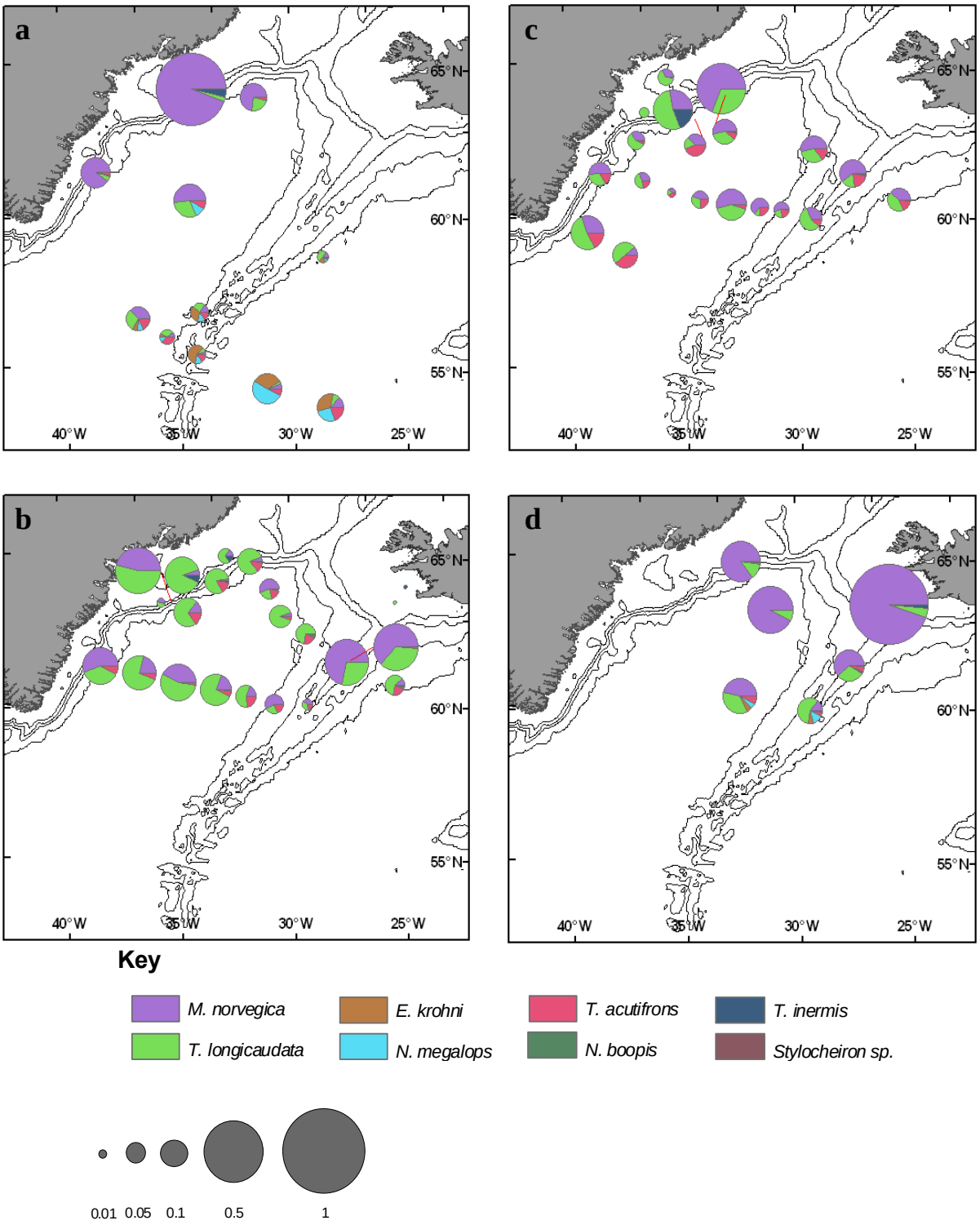

Figure 5.3. Seasonal distribution of euphausiid biomass in the Irminger Sea (between 0-800 m) during (a) D258: winter 2001/02 (b) D262: spring 2002, (c) D264: summer 2002 and (d) D267: winter 2002/03. The sizes of the pie diagrams are proportional to the log total of euphausiid biomass per net (mg m^{-3}).

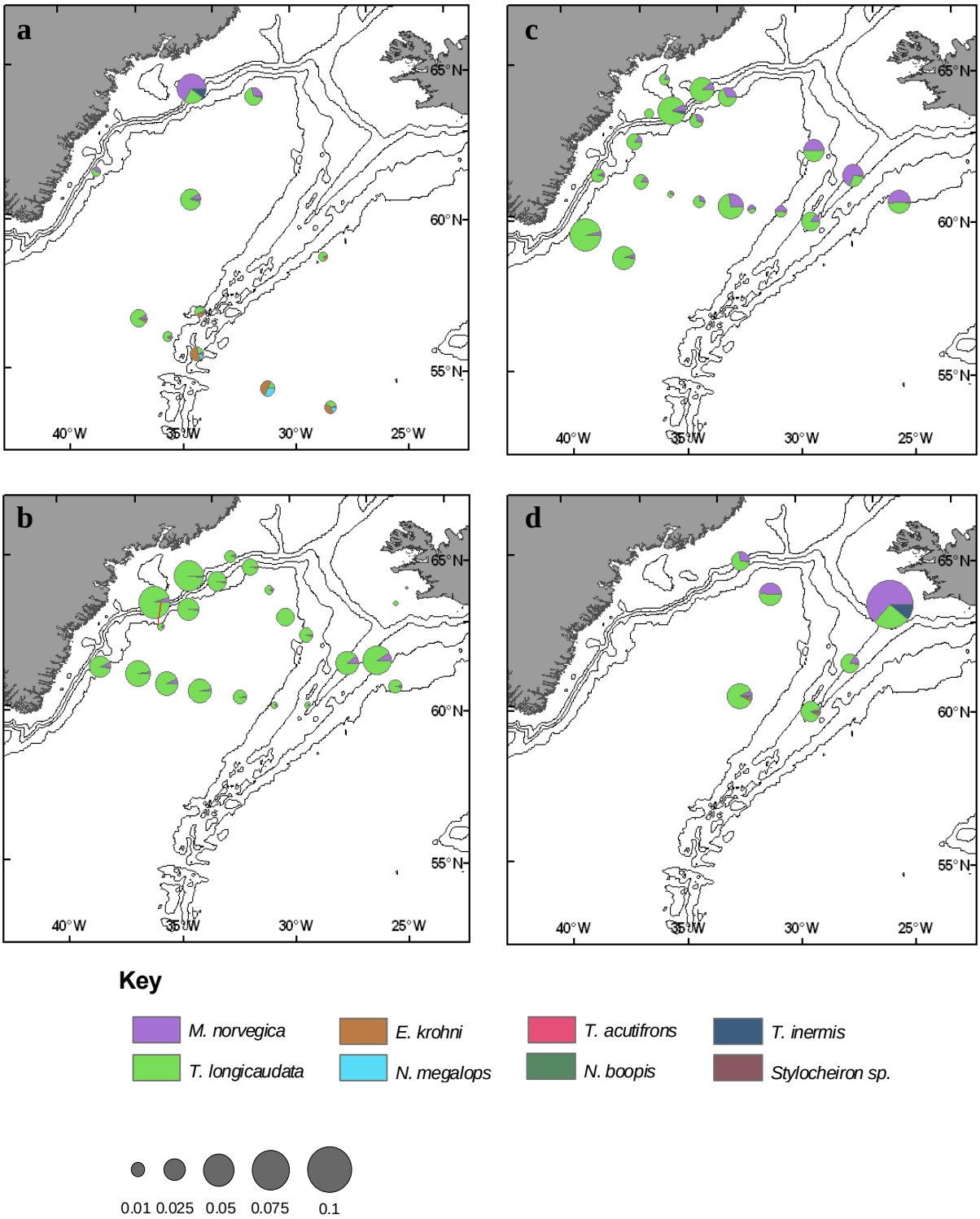

Figure 5.4. Seasonal distribution of euphausiid density in the Irminger Sea (between 0-800 m) during (a) D258: winter 2001/02 (b) D262: spring 2002, (c) D264: summer 2002 and (d) D267: winter 2002/03. The sizes of the pie diagrams are proportional to the log total of the number of euphausiids per net (ind. m^{-3}).

Other species encountered in the net samples included *Euphausia krohni*, *Nematoscelis megalops*, *Nematobrachion boopis* and *Stylocheiron* spp, which were minor in terms of numerical abundance and biomass. These species were generally restricted to the southern regions of the basin, where warmer waters associated with the Gulf Stream and North Atlantic Current typically prevail (Figures 5.3 and 5.4).

Table 5.3. Mean abundance and biomass of euphausiid species in the Irminger Sea. 56 net tows were conducted in the Irminger Sea (D258: *n* = 8, D262: *n* = 20, D264: *n* = 22, D267: *n* = 6).

Cruise	Abundance (ind. 1000 m^{-3})		Biomass (mg 1000 m^{-3})	
	Mean	Range	Mean	Range
Meganyctiphanes norvegica				
D258	47	1-294	1044	7-7228
D262	8	1-36	203	0-972
D264	31	0-151	162	0-1269
D267	194	5-962	2606	47-12818
Thysanoessa longicaudata				
D258	73	17-175	72	11-163
D262	175	15-480	274	16-749
D264	123	11-505	138	8-583
D267	196	112-397	209	109-475
Thysanopoda acutifrons				
D258	2	0-3	26	0-50
D262	1	0-3	26	0-60
D264	1	0-4	31	0-123
D267	2	0-3	19	0-51
Thysanoessa inermis				
D258	6	0-47	33	0-266
D262	1	0-7	4	0-44
D264	1	0-16	9	0-169
D267	27	0-159	42	0-241
Other spp.				
D258	12	0-57	38	0-112
D262	<1	0-1	2	0-11
D264	<1	0-1	2	0-13
D267	5	0-16	29	0-76

Seasonal trends in the variation of euphausiid abundance and biomass were difficult to elucidate given the high spatial sampling variability between cruises, the coarse

temporal resolution, and the as-expected high degree of patchiness in krill distribution and abundance. Winter stations were particularly few and spatial coverage across the Basin was low in winter (Figures 5.3 and 5.4). However, the data available suggest that there were some seasonal variations in both abundance and biomass (Table 5.3). The highest mean abundance and biomass of *M. norvegica* were attained during winter 2001/02 (47 ind. 1000 m^{-3} and 1044 1000 mg m^{-3}) and winter 2002/03 (194 ind 1000 m^{-3} and 2606 mg 1000 m^{-3}). Abundance was very low in the spring season (8 ind. 1000 m^{-3}), although the mean biomass was moderately high (203 mg 1000 m^{-3}). The mean abundance of *M. norvegica* increased in the summer, but the mean biomass was similar to that observed in spring (162 mg 1000 m^{-3}).

Seasonal variation in *T. longicaudata* biomass and abundance differed slightly from that of *M. norvegica*. The values were lowest during winter 2001/02 (72 mg 1000 m^{-3} and 73 ind.1000 m^{-3}) and the biomass maximum occurred in spring (274 mg1000 m^{-3}), when abundance was also relatively high (175 ind. 1000 m^{-3}). There was a marked decrease in biomass by the summer (138 mg 1000 m^{-3}), but the number of individuals present at this time was similar to that observed in spring (123 ind.1000 m^{-3}). Both the abundance and biomass of this species were high during the winter season in 2002/03. No seasonal variation in mean *T. acutifrons* biomass or numerical abundance was evident, and levels remained relatively uniform throughout the year.

5.4.4. Distribution of euphausiid larvae

The OCEAN sampler was only deployed on a limited number of occasions during the winter cruises due to adverse weather conditions. Bad weather also affected the extent to which ARIES could be deployed in the winter, and stations were restricted to the eastern part of the Irminger Basin. The data available indicate that some euphausiid larvae were present in the water column during the winter season (Figure 5.5). However, the main reproductive event occurred in spring, when euphausiid eggs were abundant in the upper 400 m of the water column across the Irminger Sea (Figure 5.6), and high numbers of euphausiid nauplii and calyptopis were obtained at each station between 0-800 m (Figure 5.5).

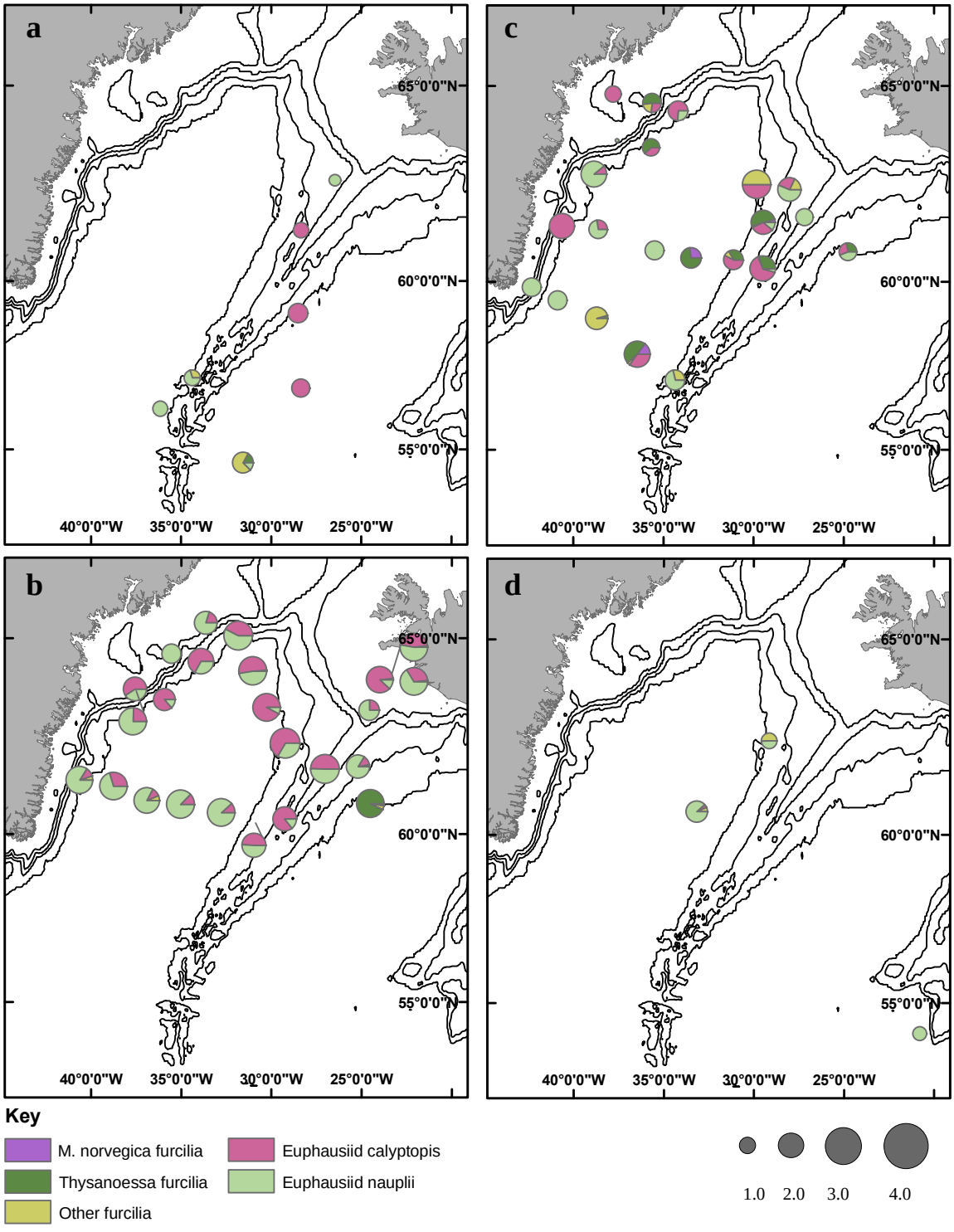

Figure 5.5. Distribution of euphausiid larvae in the Irminger Sea (between 0-800 m) collected by ARIES during (a) D258: winter 2001/02 (b) D262: spring 2002, (c) D264: summer 2002 and (d) D267: winter 2002/03. The sizes of the pie diagrams are proportional to the log total of the number of euphausiids stages per net (ind. m^{-2}).

In general, stations along the northern transect (B-line) comprised a higher proportion of euphausiid calyptopis stages than nauplii, whilst stations on the central transect (DD-line) comprised a higher proportion of nauplii. Lower catches of larvae were obtained during the summer, and eggs were absent from all but one station, indicating a limited, spring breeding season (Figures 5.5 and 5.6). Euphausiid furcilia stages were present in the water column during the summer, and *Thysanoessa* furcilia were relatively abundant. However, few *M. norvegica* furcilia were obtained during this time (Figure 5.5). Few euphausiid nauplii were obtained in the upper 400 m by the OCEAN sampler during either the spring or the summer, but data from ARIES indicated that these stages were present at approximately the same stations. This might indicate that these stages reside predominantly below 400 m. The results could also derive from differences in sampling depths or volumes between the two sampling systems.

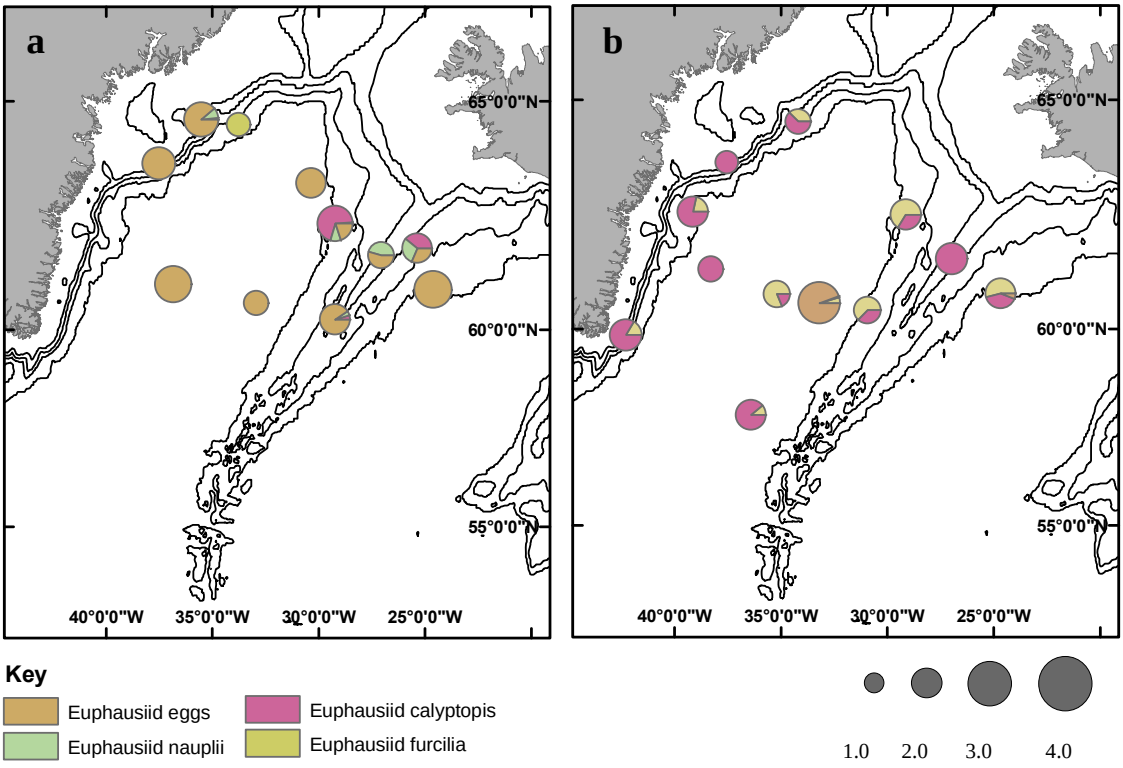

Figure 5.6. Distribution of euphausiid larvae in the Irminger Sea (between 0-400 m) collected by OCEAN sampler during (a) D262: spring 2002 and (b) D264: summer 2002. The sizes of the pie diagrams are proportional to the log total of the number of euphausiids stages per net (ind. m^{-2}).

5.4.5. Regional population analysis

Hierarchical cluster analyses were conducted on the relative length-frequency data for *M. norvegica* and *T. longicaudata* in the spring and summer seasons. Data from summer (D264) were used for *M. norvegica*, because there were more stations with >60 individuals. All clusters were defined at the same Euclidean distance (distance = 6). The results indicate three regions within the Irminger Sea where the population structures of each species were homogenous; a central region (DD-line), northern region (B-line) and an East Greenland shelf region (C-line) (Figures 5.7 and 5.8). These biological regions corresponded broadly with oceanographically distinct zones within the basin. The central zone and northern region identified in this investigation were situated in Central Irminger Sea water and the North Irminger current, respectively. The East Greenland shelf slope region was predominantly located within the highly dynamic East Greenland Current.

The year class terminology used by Einarsson (1945), Falk-Petersen & Hopkins (1981) and Tesch (1971) has been adopted to describe the population structure; i.e., individuals are said to belong to a 0-group from the time of hatching until March of the following year, to a I-group from 1 April to 30 March the next year, and so on. The general life span of *M. norvegica* in the Irminger Sea was two years (Figure 5.9 and Table 5.4). Through a large part of the year the population was comprised of 2 size, and presumably age classes; juveniles <1 year old (0-group) and 1+ year olds (I-group). The stock in spring consisted of I-group and II-group (2 years old) krill. The majority of individuals in both of these groups were sexually mature adults bearing spermatophores, indicating the main spring reproductive event (Figures 5.9 and 5.10). No furcilia stages were present in the water column during this time (Figure 5.5). By summer, the newly spawned individuals were evident as the juvenile 0-group, which formed the highest proportion of the population (Table 5.4). A large proportion of the II-group had presumably died by this time, and the larger krill present are assumed to have been mainly I-group. If II-group individuals were present, they were indistinguishable from the I-group individuals in terms of body length. None of these I-group (or possibly II-group) animals bore spermatophores, indicating that the reproductive season had ended by summer (Figure 5.10). Most of the newly spawned

0-group individuals increased in size between the summer and winter, but spent their first winter as either juveniles or sub-adults.

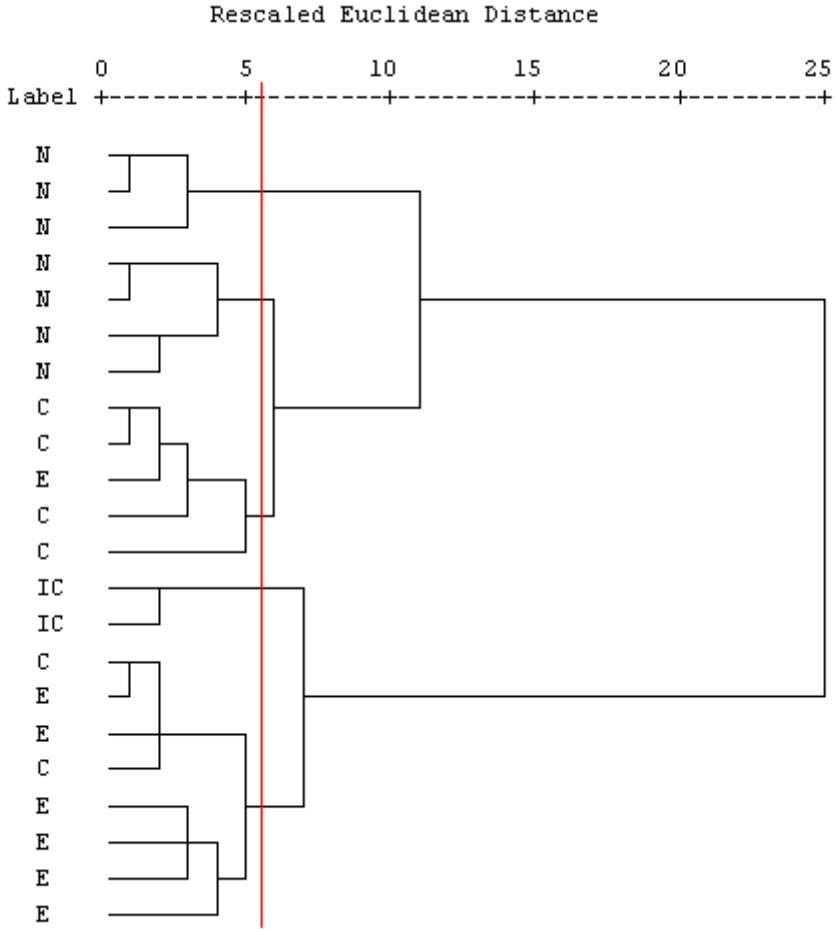

Figure 5.7. Dendrogram of *T. longicaudata* relative length-frequency data during spring D262. Stations in the Northern, Central and E. Greenland Coast region are denoted "N", "C" and "E", respectively. "IC" denotes stations around the Icelandic Coast.

There were regional differences in the length-frequency distribution of *M. norvegica* within the Irminger Sea (Figure 5.9). Around the East Greenland Coast there were mostly 2 cohorts present, the 0-group and the I-group or II-group. The cohort with the largest bodies comprised between 29 and 50% (numerically) of the total population throughout the year in this region (Table 5.4). However, in the Central region and the Northern region, there were comparatively fewer large individuals during much of the year. The I-group cohort made up a very low percentage in the Northern region during summer and both winters, and formed just 7-17% (numerically) of the population in the Central region during the same seasons (Table 5.4). There was some

evidence of interannual and regional differences in the modal size of the 0-group cohort throughout the Irminger Sea (Figure 5.9 and Table 5.4). For example, the 0-group was almost 3.5 mm smaller in the EGC region than in the Central and Northern regions in winter 2002, and the equivalent year-group was considerably smaller in winter 2002 than in winter 2001 (the modes being 20.4 mm and 25.5 mm, respectively). These results are, however, slightly ambiguous and difficult to interpret because during each of the four cruises, there was a temporal mismatch in sampling dates (up to 16 days) between regions. The likely growth increment during this time would be between ~1.0 and 4.8 mm (cf. Table 5.6).

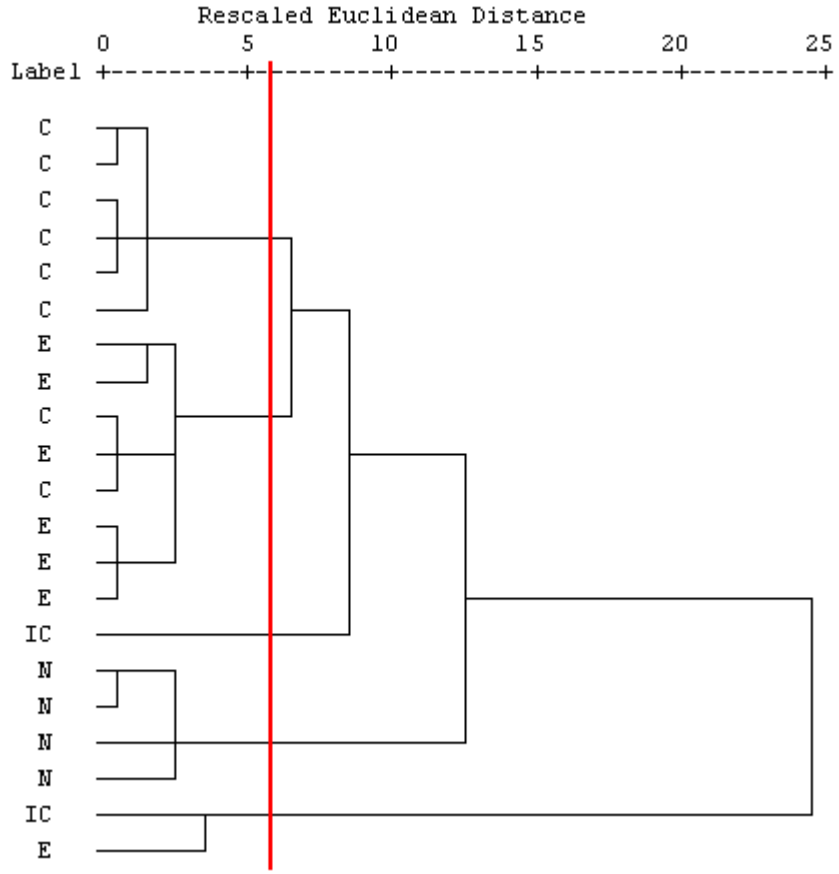

Figure 5.8. Dendrogram of *M. norvegica* relative length-frequency data during spring D262. Stations in the Northern, Central and E. Greenland Coast region are denoted “N”, “C” and “E”, respectively. “IC” denotes stations around the Icelandic Coast.

Regional and inter-annual differences in modal size were less obvious for *T. longicaudata* than for *M. norvegica* (Figure 5.11 and Table 5.5). In the Central and Northern region an annual life cycle was evident. Almost all animals had spermatophores in spring when they attained sexual maturity at one year of age (I-

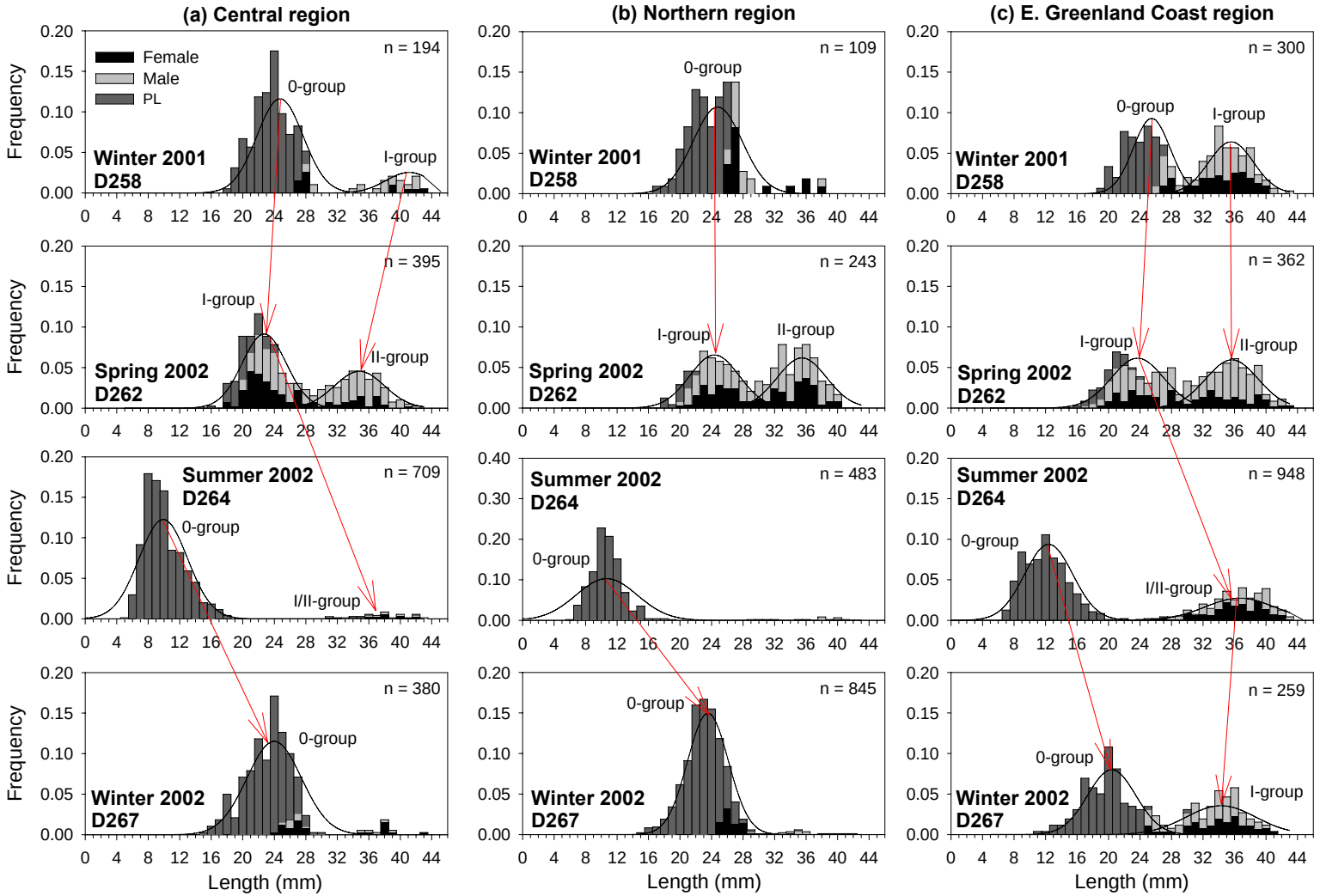

Figure 5.9. Seasonal length-frequency distribution of *M. norvegica* in (a) the Central region, (b) Northern region and (c) EGC region.

Table 5.4. Fitted components for *M. norvegica* using CMIX software (see Materials and methods). CMIX could only fit one distribution to the data denoted by *

Region	Cruise	Best fit no. components	0-group μ (mm) (±S.E.)	0-group σ (mm)	0-group proportion (±S.E.)	I-group μ (mm) (±S.E.)	I-group σ (mm)	I-group proportion (±S.E.)	II-group μ (mm) (±S.E.)	II-group σ (mm)	II-group proportion (±S.E.)
Central	D258	2	24.7 (0.2)	2.9	0.82 (0.01)	41.1 (0.2)	2.9	0.17 (0.01)	n/a	n/a	n/a
	D262	2	n/a	n/a	n/a	22.7 (0.1)	2.8	0.64 (0.01)	34.8 (0.2)	3.1	0.36 (0.01)
	D264	2	9.9 (0.1)	3.1	0.93 (0.01)	40.8 (0.2)	6.1	0.07 (0.01)	n/a	n/a	n/a
	D267	1*	24.0 (0.2)	3.4	1.00	n/a	n/a	n/a	n/a	n/a	n/a
Northern	D258	1*	24.8 (0.3)	3.1	1.00	n/a	n/a	n/a	n/a	n/a	n/a
	D262	2	n/a	n/a	n/a	24.4 (0.2)	3.1	0.51 (0.1)	35.5 (0.2)	0.4	0.49 (0.01)
	D264	1*	10.7 (0.2)	3.9	1.00	n/a	n/a	n/a	n/a	n/a	n/a
	D267	1*	23.5 (0.1)	2.6	1.00	n/a	n/a	n/a	n/a	n/a	n/a
EGC	D258	2	25.5 (0.1)	2.3	0.54 (0.06)	35.6 (0.2)	2.8	0.46 (0.002)	n/a	n/a	n/a
	D262	2	n/a	n/a	n/a	23.7 (0.2)	3.3	0.50 (0.01)	35.6 (0.2)	3.3	0.50 (0.007)
	D264	2	12.4 (0.1)	3.0	0.71 (0.005)	36.7 (0.2)	4.4	0.29 (0.002)	n/a	n/a	n/a
	D267	2	20.4 (0.2)	3.0	0.61 (0.01)	34.3 (0.3)	4.4	0.39 (0.005)	n/a	n/a	n/a

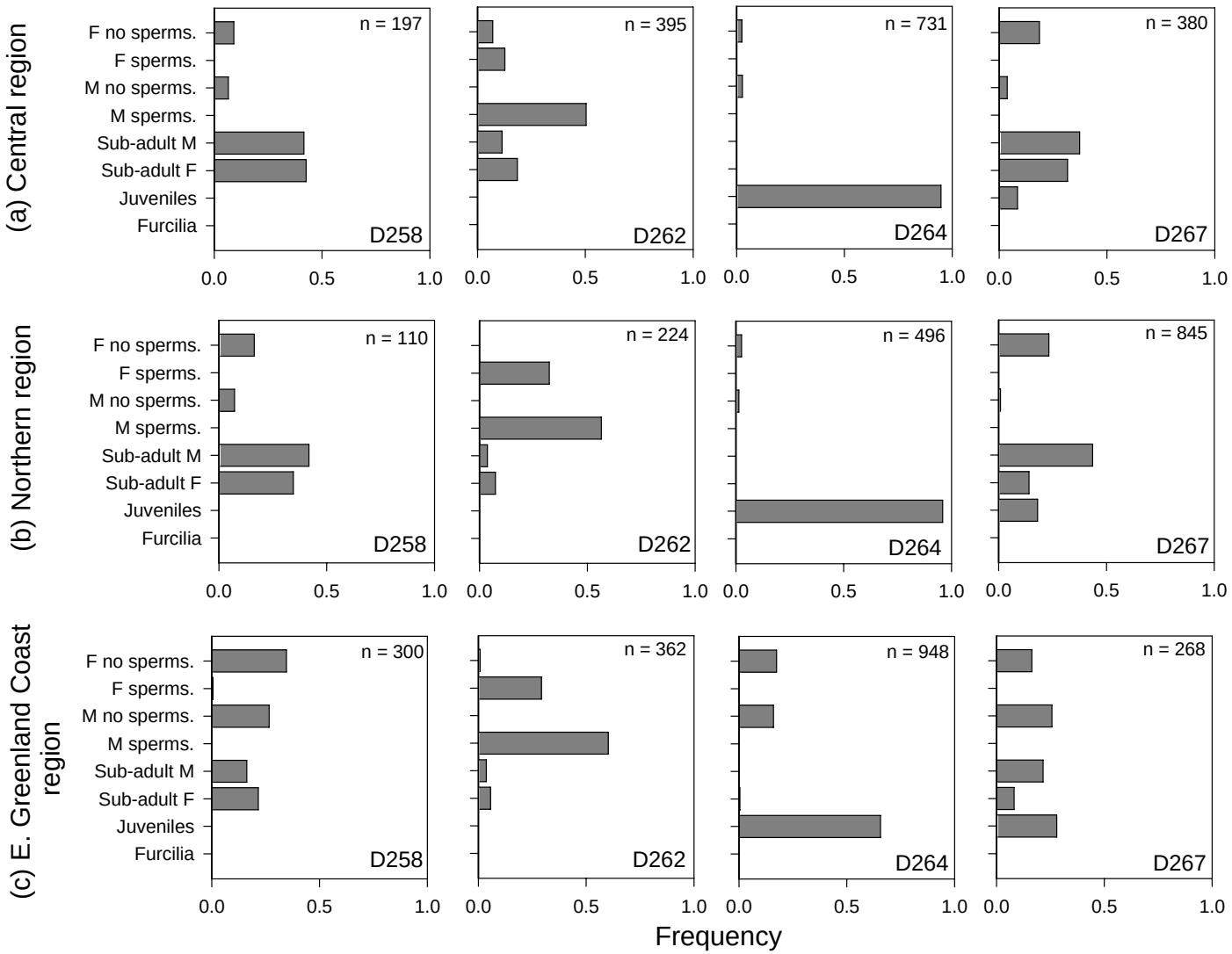

Figure 5.10. Sex and maturity status of *M. norvegica* in (a) the Central Irminger Basin, (b) the North Irminger Basin and (c) the E.Greenland Coast region during 2001-2002. Abbreviations in the legend are: Sub-adult F (Sub-adult female), Sub-adult M (Sub-adult male), M sperms (Adult male with spermatophores at the gential aperture or petasma), M no sperms (Adult male without external spermatophores), F sperms (Adult female with spermatophores), and F no sperms (Adult female without spermatophores).

group; Figure 5.12). During this time a new brood was spawned (0-group), which became evident in the Dual Methot net samples in summer, comprising the largest proportion of the population (77-88%). The majority of the I-group spawning stock had vanished by the summer season, presumably having died post-spawning. However, the proportion of the I-group cohort remaining in the population was slightly higher in the Northern sector of the Basin than in the Central zone (Figure 5.11). Relatively few animals had spermatophores by late summer, and the population was comprised largely of post-larval stages (Figure 5.12). The remaining I-group cohort had disappeared completely from the population by winter, and the 0-group individuals present at this time over-wintered as immature post-larvae, presumably later to become the next spawning cohort in the following spring. The length frequency distribution of *T. longicaudata* was different in the East Greenland Coast region. In each season there were predominantly two cohorts present in the population, the oldest contributing around 10-30% of the population (Figure 5.11, Table 5.5). The demise of the I-group following the spring spawning event was far less pronounced than in the Northern and Central regions. The presence of a second cohort in both winter periods, and during spring, suggests that animals in this region persisted for up to two years, whereas they only persisted just over one year in the other sectors of the Irminger Sea.

5.4.6. Regional sexual maturity status

There were no obvious regional differences in the sexual maturity status of *T. longicaudata* in the Irminger Sea throughout the year (Figure 5.12). The proportions of each maturity stage in all three regions were relatively similar in winter, spring, and summer, respectively, and the results show no evidence of inter-annual differences between 2001 and 2002. To a large extent, the *M. norvegica* results (Figure 5.10) reflect the fact that there was an older age group (I-group) present in the population around the East Greenland Coast region throughout the year, whereas there were typically only younger (0-group) *M. norvegica* in the other regions. There was some evidence of regional differences in the maturity status of *M. norvegica* during spring (D262), when there were proportionally fewer adult females bearing spermatophores

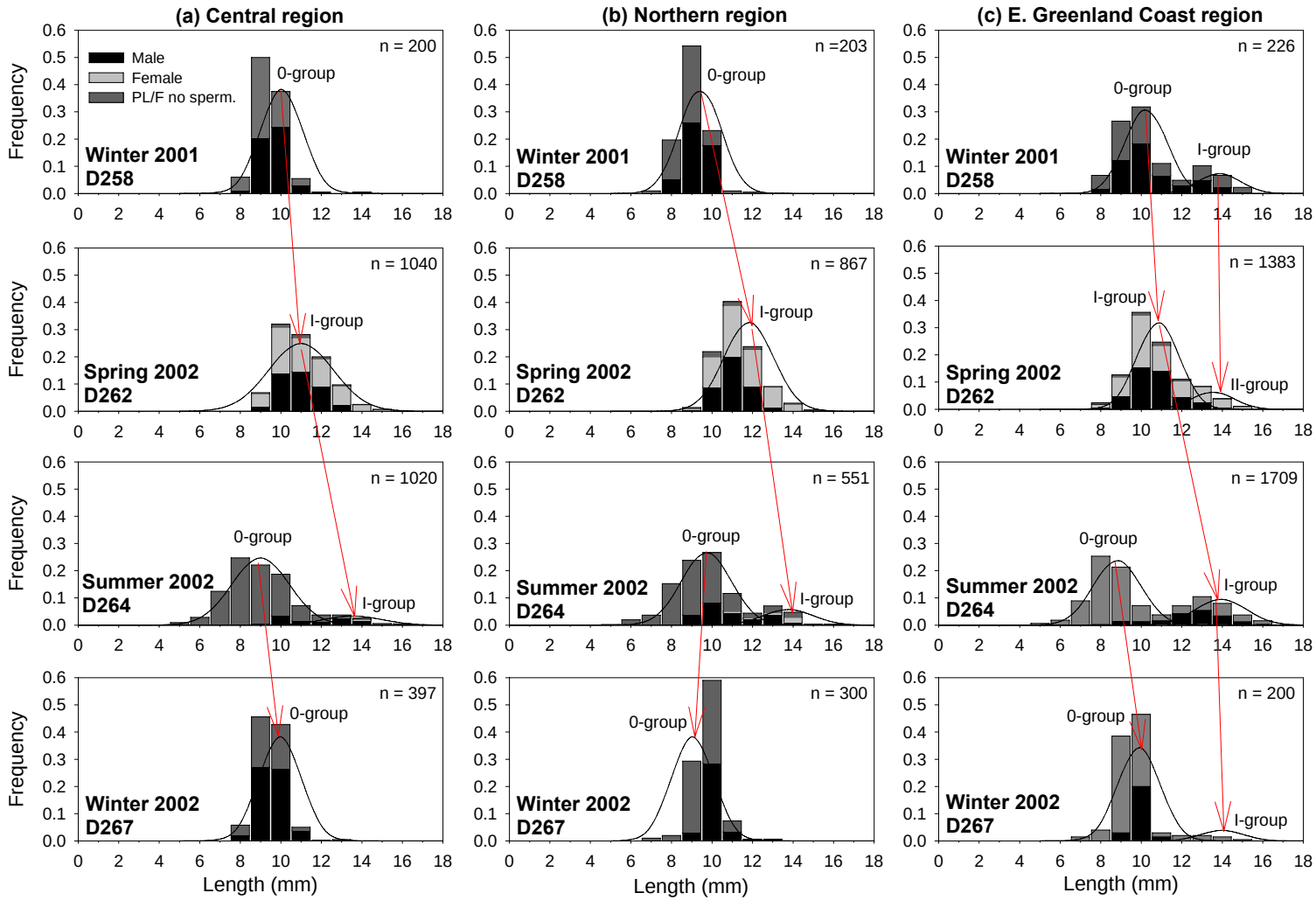

Figure 5.11. Seasonal length-frequency distribution of *T. longicaudata* in (a) the Central region, (b) Northern region and (c) EGC region.

Table 5.5. Fitted components for *T. longicaudata* using CMIX software (see Materials and methods).

Region	Cruise	Best fit no. comp.	0-group μ (mm) (±S.E.)	0-group σ (mm)	0-group proportion (±S.E.)	I-group μ (mm) (±S.E.)	I-group σ (mm)	I-group proportion (±S.E.)	II-group μ (mm) (±S.E.)	II-group σ (mm)	II-group proportion (±S.E.)
Central	D258	1	10.0 (0.1)	1.0	1.00	n/a	n/a	n/a	n/a	n/a	n/a
	D262	1	n/a	n/a	n/a	11.0 (0.05)	1.6	1.00	n/a	n/a	n/a
	D264	2	9.0 (0.04)	1.4	0.88 (0.01)	13.6 (0.04)	1.4	0.12 (0.004)	n/a	n/a	n/a
	D267	1	10.0 (0.05)	1.0	1.00	n/a	n/a	n/a	n/a	n/a	n/a
Northern	D258	1	9.4 (0.07)	1.0	1.00	n/a	n/a	n/a	n/a	n/a	n/a
	D262	1	n/a	n/a	n/a	11.8 (0.04)	1.2	1.00	n/a	n/a	n/a
	D264	2	10.0 (0.06)	1.4	0.77 (0.006)	13.5 (0.06)	1.4	0.23 (0.004)	n/a	n/a	n/a
	D267	1	9.0 (0.06)	1.0	1.00				n/a	n/a	n/a
EGC	D258	2	10.2 (0.07)	1.0	0.81 (0.003)	13.8 (0.07)	1.0	0.19 (0.003)	n/a	n/a	n/a
	D262	2	n/a	n/a	n/a	10.8 (0.03)	1.0	0.83 (0.004)	13.5 (0.03)	1.0	0.17 (0.002)
	D264	2	8.8 (0.03)	1.1	0.70 (0.004)	13.9 (0.03)	1.2	0.30 (0.003)	n/a	n/a	n/a
	D267	2	9.9 (0.07)	1.0	0.90 (0.001)	14.0 (0.07)	1.0	0.10 (0.003)	n/a	n/a	n/a

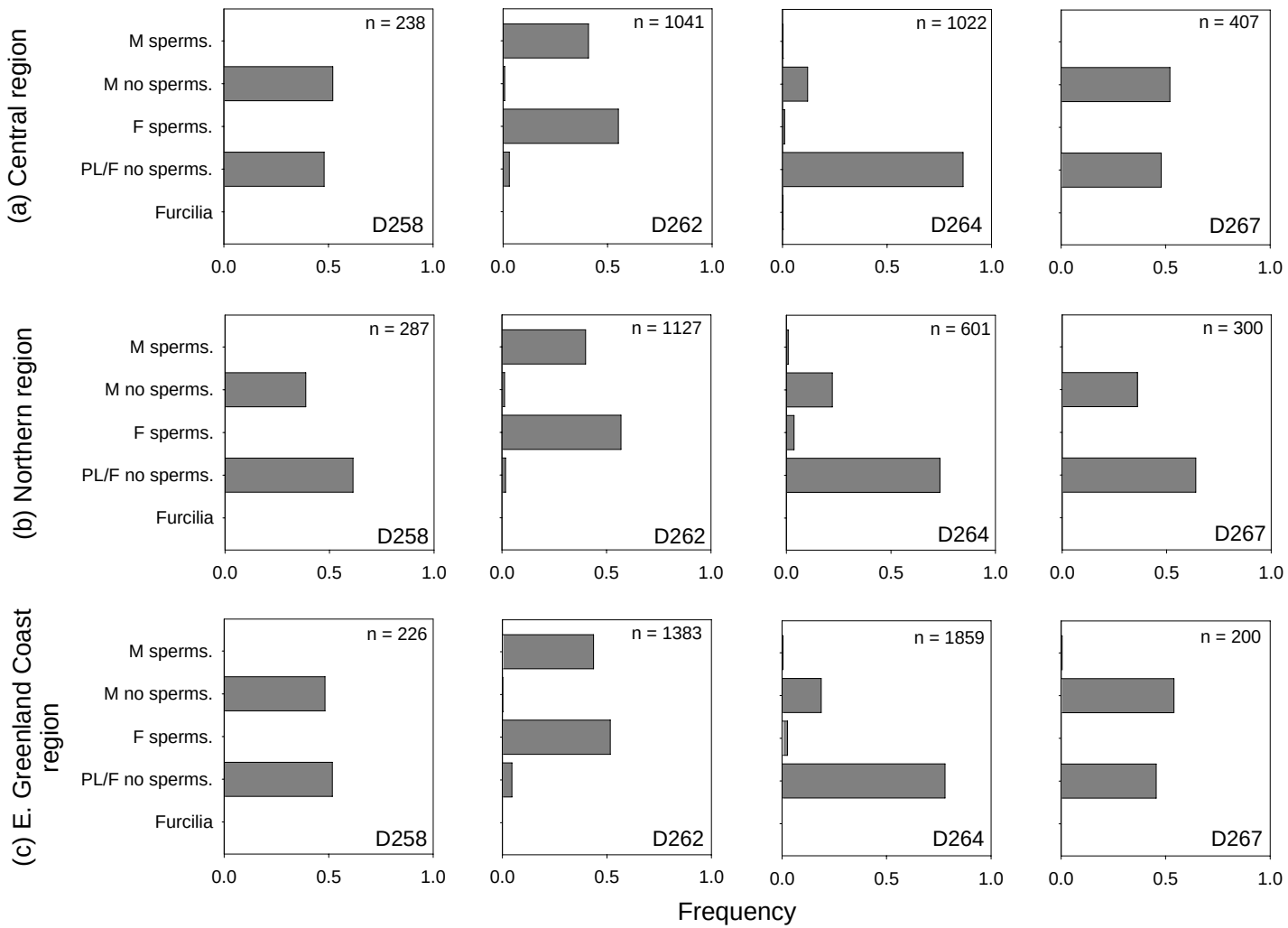

Figure 5.12. Sex and maturity status of *T. longicaudata* in (a) the Central Irminger Basin, (b) the North Irminger Basin and (c) the E.Greenland Coast region during 2001-2002. Abbreviations in the legend are: PL/F no sperms (Post larvae and females without spermatophores), F sperms (Adult female with spermatophores), M no sperms (Adult male without external spermatophores), and M sperms (Adult male with spermatophores at the gential aperture or petasma).

in the Central region than in the Northern and East Greenland Coast regions (Figure 5.10). Correspondingly, the proportion of sub-adult males and females was higher in the Central region, suggesting that fewer krill had reached sexual maturity by the spring. Other differences in development status of the species were evident between winter 2001/02 (D258) and winter 2002/03 (D267). There were more juvenile krill in the water column during in winter 2002/03 than in winter 2001/02. The majority of non-adult krill had advanced to a sub-adult stage by winter 2001/02.

5.4.7. Growth

In all regions, there was no positive growth for *M. norvegica* between winter 2001 and spring 2002 (Table 5.6). All *M. norvegica* cohorts regressed in size during this period, except for the I-group cohort in the EGC region, which stayed the same size. Overall, growth rates were mainly positive in the Irminger Sea following the spring season, with values around 0.08-0.19 mm d^{-1} (0.6-1.2% per day). The results show some evidence for regional differences in growth of *M. norvegica*, which was marginally lower in the EGC region than in the Central and Northern regions. Growth of *T. longicaudata* was mostly positive throughout the year, with rates of growth of around <0.01-0.03 mm d^{-1} (approximately 0.05-0.3% per day; Table 5.7). In all regions and for both species, the highest rates of growth occurred between spring and summer for the I-group year class. Comparatively, growth was lower between winter-spring and summer-winter. Growth of *M. norvegica* and *T. longicaudata* was not significantly (P>0.05) correlated with either mean temperature or mean chlorophyll *a* concentration in any of the depth strata investigated.

5.5. Discussion

5.5.1. Patch dynamics

Krill abundance, distribution and life cycle patterns are patchy and highly variable in space and time, even within relatively small pelagic ecosystems (see review by Siegel, 2000). An underlying assumption of population dynamical studies in deepwater

pelagic communities is that the individuals sampled throughout the investigation are from the same population (Falk-Petersen and Hopkins 1981). This assumption is generally valid for semi-enclosed systems such as fjords, but probably less so for large and highly dynamic ocean systems such as the Irminger Sea (Nicol 2000). Horizontal displacement that continually shifts water masses may be further complicated by diurnal vertical migrations (Tarling et al. 1999) that expose organisms to different current regimes at different depths (Bryant et al. 1998). Considering that the data presented here were collected at low temporal and spatial resolution, these factors need to be taken into account when interpreting the results of this investigation.

Table 5.6. Regional growth rates of *M. norvegica* in the Irminger Sea region during 2001-2002. Minimum and maximum growth rates are the 95% confidence intervals

Region	Cruise	Date	No. days	Growth rate of 0-group (mm/d)	Minimum growth rate of 0-group (mm/d)	Maximum growth rate of 0-group (mm/d)	Growth rate of I-group (mm/d)	Minimum growth rate of I-group (mm/d)	Maximum growth rate of I-group (mm/d)
Central	D258-D262	12/11/01 to 04/05/02	165	-0.0121	-0.0797	0.0555	-0.0381	-0.1100	0.0339
	D262-D264	04/05/02 to 05/08/02	94	na	na	na	0.1929	0.0081	0.3776
	D264-D267	05/08/02 to 30/11/02	118	0.1197	0.0110	0.2283	na	na	na
Northern	D258-D262	29/11/01 to 19/05/02	172	-0.0023	-0.0731	0.0686	na	na	na
	D262-D264	19/05/02 to 31/07/02	74	na	na	na	na	na	na
	D264-D267	31/07/02 to 20/11/02	113	0.1139	0.0022	0.2256	na	na	na
EGC	D258-D262	01/12/01 to 13/05/02	164	-0.0110	-0.0782	0.0561	0.0005	-0.0730	0.0740
	D262-D264	13/05/02 to 16/08/02	96	na	na	na	0.1357	0.0061	0.2654
	D264-D267	16/08/02 to 21/11/02	98	0.0822	-0.0394	0.2038	-0.0245	-0.1735	0.1245

5.5.2. Distribution of abundance and biomass

Spatial heterogeneity was apparent in euphausiid species distribution in the Irminger Basin, but our observations are in broad agreement with previous, albeit limited, findings. *Meganyctiphanes norvegica* was confined to the North Atlantic and adjacent seas and was most common over continental slopes, oceanic ridges and deep continental shelf waters, occurring at depths between 100-500 m (Einarsson 1945; Mauchline and Fisher 1969). *Thysanoessa longicaudata* is the most abundant euphausiid in the oceanic surface waters of the boreal North Atlantic, but it is

confined within this region. Lindley (1977), using data from CPR surveys, noted that the main centre of abundance of the species lies over the deep and colder waters of the Labrador-Irminger Gyre. *Thysanopoda acutifrons* has been described as bathypelagic, with animals typically caught between 140 to 4000 m, and adults often occurring below 2000 m (Einarsson 1945). Other oceanic species, such as *E. krohni* and *N. megalops*, are typically associated with temperate to warm North Atlantic waters, whilst *T. inermis* is often most abundant in more coastal waters around the Icelandic coast and East Greenland shelf-break (Astthorsson 1990; Astthorsson and Gislason 1997).

Table 5.7. Regional growth rates of *T. longicaudata* in the Irminger Sea region during 2001-2002. Minimum and maximum growth rates are the 95% confidence interval.

Region	Cruise	Date	No. days	Growth rate of 0-group (mm/d)	Minimum growth rate of 0-group (mm/d)	Maximum growth rate of 0-group (mm/d)	Growth rate of I-group (mm/d)	Minimum growth rate of I-group (mm/d)	Maximum growth rate of I-group (mm/d)
Central	D258-D262	12/11/01 to 04/05/02	165	0.0059	-0.0246	0.0364	na	na	na
	D262-D264	04/05/02 to 05/08/02	94	na	na	na	0.0272	-0.0339	0.0883
	D264-D267	05/08/02 to 30/11/02	118	0.0081	-0.0309	0.0472	na	na	na
Northern	D258-D262	29/11/01 to 19/05/02	172	0.0141	-0.0108	0.0389	na	na	na
	D262-D264	19/05/02 to 31/07/02	74	na	na	na	0.0220	-0.0452	0.0893
	D264-D267	31/07/02 to 20/11/02	113	-0.0087	-0.0494	0.0321	na	na	na
EGC	D258-D262	01/12/01 to 13/05/02	164	0.0037	-0.0202	0.0276	-0.0019	-0.0258	0.0220
	D262-D264	13/05/02 to 16/08/02	96	na	na	na	0.0319	-0.0137	0.0774
	D264-D267	16/08/02 to 21/11/02	98	0.0111	-0.0317	0.0539	0.0009	-0.0437	0.0455

Throughout our sampling regime, the stations that comprised the highest euphausiid abundance and biomass in the Irminger Basin were generally situated around the East Greenland Shelf break, a region where water mixed from the East Greenland Current and the Northern Irminger Current predominates. Einarsson (1945) also reported that the abundance of euphausiids, principally *T. longicaudata*, was highest in this mixed water region, while stations lying inside the East Greenland Current proper showed low numbers of individuals. Other regions of high biomass and abundance included the Iceland shelf and the northern section of the Reykjanes Ridge. These shallow regions have very different oceanographic regimes compared to the open ocean and East Greenland Shelf break, and are often associated with higher zooplankton

abundance, biomass and production (Gislason and Astthorsson 1995). As a consequence, there is high fisheries production (Cushing 1990; Sigurdsson et al. 2006).

Estimates of seasonal euphausiid abundance and biomass in the Irminger Sea are scarce and previous estimates are difficult to compare with results from this investigation. Data from Einarsson (1945) were in many respects limited, having been collected over several years, with various sampling gears, and not including a series of samples from any one area. Estimates of abundance and biomass of *T. longicaudata* in our investigation were considerably lower than those reported from the CPR surveys in proximity to the Irminger Basin (Lindley 1978), but this may be attributed to differences in sampling methods between the two studies. The abundance of *M. norvegica* in the Irminger Sea in this study was similar to that observed from the waters north of Iceland (up to 73 ind. 1000 m^{-3}; Astthorsson & Gislason, 1997) and in the Skagerak (Buchholz and Boysen-Ennen 1988). However, the abundance was around an order of magnitude lower than that reported for the same species from the Läsö-Deep in the Kattegat (Boysen and Buchholz 1984; Buchholz and Boysen-Ennen 1988). Marked inter-annual variations in standing stocks of this species have also been reported in both the Skagerak and Kattegat (Ulmestrand and Hagström 1992). Elsewhere in the North Atlantic, Dalpadado & Skjoldal (1996) showed that there were marked annual and seasonal fluctuations in mean *T. longicaudata* abundance and biomass in the Barents Sea during 1984-1992 (between 1.9-225 ind. 1000 m^{-3} and 6-298 mg 1000 m^{-3}). The results of the present investigation are consistent with this level of variation.

Patterns we observed of seasonal fluctuation in euphausiid abundance and biomass in the Irminger Sea agree generally with studies from around Iceland and various regions of the North Atlantic (Astthorsson and Gislason 1997; Lindley 1978). These patterns are also consistent with the expected life cycles and behaviour of the dominant northern euphausiid species. In part, the seasonal changes observed for *T. longicaudata* and *M. norvegica* reflect pre-spawning aggregations of euphausiids in late winter, their dispersion and increased mortality after spawning, and subsequent growth and recruitment in the following spring and summer (Mauchline 1980a; Mauchline and Fisher 1969). The seasonal estimates of abundance and biomass,

however, may incur a wide margin of error due to the high spatial variability along the sampling transects and the high degree of patchiness in euphausiid distribution throughout the region. Previous investigations of euphausiids at high latitudes have noted that seasonal changes in biomass and abundance may also reflect difficulties in sampling euphausiids quantitatively because of net avoidance and behaviour in relation to seasonal changes in light conditions (Falk-Petersen and Hopkins 1981). Such studies imply that this group may have been under sampled during the summer compared to the winter, as the high light intensity and extended hours of daylight in summer may drive the krill towards the sea floor (Astthorsson and Gislason 1997; Dalpadado and Skjoldal 1996; Falk-Petersen and Hopkins 1981). These other studies were, however, conducted in relatively shallow fjordic systems. The net samples in this investigation were obtained predominantly in deeper, open water and nets were integrated over 0-800 m of the water column, thus covering the maximum expected distributional ranges of most euphausiid species in the region (Mauchline and Fisher 1969). Furthermore, euphausiid abundance and biomass were significantly higher in the 0-400 m depth strata than in the 400-800 m strata in all nets taken during hours of daylight, indicating that the majority of euphausiids did not occur much deeper than 400 m during seasons of high light intensity, and that the effect of diel vertical migration regimes on the results was minimal. This is consistent with acoustic observations and net data obtained throughout the area sampled (Anderson et al. 2005; Gislason et al. 2006).

5.5.3. Distribution of larvae

Our data comprise the first broad-scale observations of the distribution and abundance of euphausiid larval stages in the Irminger Sea during the winter and the spring. Previous investigations in the area were restricted to late summer (Einarsson 1945). Several authors have noted a close relationship between the spawning of northern euphausiids and the onset of the spring phytoplankton bloom (Astthorsson 1990; Dalpadado and Skjoldal 1996; Einarsson 1945; Falk-Petersen and Hopkins 1981). Lindley (1978) also noted a correlation between the timing of reproduction of *T. longicaudata* and mean sea-surface temperature, suggesting that sexual maturation is controlled mainly by temperature. To some extent, results from this investigation also

infer a relationship between spring phytoplankton growth and spawning of euphausiids at high latitudes, in that breeding mainly occurred during spring when chlorophyll *a* concentration started to increase. During this time, the abundances of euphausiid eggs, nauplii and calyptopis were maximal throughout the Irminger Sea, and the majority of adults were carrying spermatophores. The results suggest that spawning occurred throughout the Irminger Sea and was not confined to any particular region. However, further differentiation of the larvae is required to quantify species-specific spawning patterns, and analyses are ongoing. There was also some evidence of spatial heterogeneity in the distribution and abundance of the larval stages during spring and summer seasons. For example, the Northern region had proportionally less nauplii than calyptopis stages when compared to the Central Irminger Sea. This might indicate variation in development times due to different physical regimes, or regional differences in the timing and duration of spawning.

5.5.4. Population dynamics

We observed that the length-frequency distributions for *T. longicaudata* in the Northern and Central Irminger Sea were consistent with previous investigations in the region (Einarsson 1945; Lindley 1978). The results were also consistent with studies conducted in Korsfjorden, western Norway, and off northern Iceland (Astthorsson and Gislason 1997; Jörgensen and Matthews 1975). In general, these authors showed that *T. longicaudata* in these northern waters had an annual life cycle, with the life span of an individual being from 12 to 16 months. The species reaches sexual maturity at around one year of age (when body length exceeds 10 mm) and produces a new generation during a single spawning pulse during late April to late May. In contrast, Lindley (1978) observed that *T. longicaudata* produces discrete generations during two annual spawning pulses in the warmer waters of the eastern N. Atlantic. The first generation is spawned during springtime. These animals reach sexual maturity and breed by autumn, giving rise to a second generation that overwinters and breeds in the following spring. Our investigation, however, showed no evidence of two spawning events in the Irminger Sea. The population structure of *T. longicaudata* was considerably different around the East Greenland shelf break compared to the rest of the Irminger Sea. The population was predominantly bimodal at the East Greenland

shelf break, indicating that this species lived longer there than in the Central and Northern regions, with a life span extending up to two years. This is in accord with Einarsson (1945), who similarly observed the presence of two size groups in the more northern waters off East Greenland, but only one size group in the eastern part of the Denmark Strait and Irminger Sea. Dalpadado and Skjoldal (1996) have shown that *T. longicaudata* lives for around two years in the Barents Sea.

The life cycles of other northern species in the genus *Thysanoessa* appear to be adaptations to different oceanographic conditions at different latitudes within the boreal to Arctic regions of both the Atlantic and Pacific (see review by Siegel, 2000b). *Thysanoessa inermis* and *T. raschii*, demonstrate strong plasticity in age structure and maturity development, and individuals attain a greater maximum age in the Arctic and subarctic than at their southern distribution limits (Dalpadado and Skjoldal 1996; Falk-Petersen and Hopkins 1981; Jörgensen and Matthews 1975; Kulka and Corey 1978; Lindley 1980). Thus conditions appear to be more favourable for the survival of *T. longicaudata*, *T. inermis* and *T. raschii* in the colder water and at higher latitudes, where individuals grow to larger size and older age at maturation. Slow growth and larger maximal size are common features of high latitude species (Peck et al. 2004). The contrasting situation occurring around the East Greenland shelf, compared to the rest of the Irminger Sea, may be explained in terms of the prevailing ocean currents in the region. The East Greenland Current, which is persistent along the length of the Greenland continental slope, carries predominantly cold and mixed water of polar origin from the Arctic and Nordic Seas (Lavender et al. 2000). It is, therefore, probable that a large proportion of the population observed around the East Greenland shelf was advected into the region from waters farther north, where individuals typically grow larger and live to older ages due to different environmental conditions (temperature and food availability) and physiological adaptations. Given that the East Greenland shelf is a highly dynamic region, and that its waters are mixed from several sources, complex interactions could influence the population dynamics of *T. longicaudata* there.

The general life cycle pattern of *M. norvegica* throughout the Irminger Sea region was similar to that reported in previous investigations. In the waters around Scotland, Iceland and Norway, *M. norvegica* reaches sexual maturity after 1 year and

individuals survive for approximately 2 years (Einarsson 1945; Falk-Petersen and Hopkins 1981; Matthews 1973; Mauchline 1960). These authors observed a long and broadly defined spawning period, from the end of March to the end of July. Two distinct peaks of spawning have, however, been described in the Clyde Sea Area (Mauchline and Fisher 1969). Although the general life history of *M. norvegica* fits the patterns previously described, there were some regional differences in population structure within the Irminger Sea. The most notable difference was the distinct absence of individuals from the I-group cohort in the open Irminger Sea compared to the region around the East Greenland Shelf break in all seasons except the springtime. The results suggest that there was a large decline of the I-group following the spring reproductive event in the Central and Northern region, a decline not occurring in the East Greenland Coast region. Furthermore, the absence of the I-group in the Central and Northern regions in winter 2001/02 suggests that the demise of this cohort might also have occurred following spring 2001.

Possible explanations for this might be that environmental conditions were less favourable for the survival of the larger individuals in the open ocean regions than around the shelf-break, or that predation pressure was greater in the central Basin during spring to summer. Redfish (*Sebastes* sp.) are significant predators of euphausiids (Gonzalez et al. 2000). Although the distribution and abundance of redfish species are complicated in the Irminger Sea, fisheries research surveys generally show that “Pelagic deep-sea” *Sebastes mentella* and “Oceanic” *Sebastes mentella* are concentrated in the northeastern and central-southwest sectors of the Irminger Sea, respectively (Anon. 2004). Thus predation pressure may be higher in these regions than over the East Greenland shelf. Oceanographic studies conducted by Holliday et al. (2006) during our investigation show that, although the Central and Northern regions had very different physical conditions, the spring phytoplankton bloom in the both areas was low, with consistently low chlorophyll *a* concentration persisting throughout the year (see SeaWifs images in Sanders et al., 2005). In contrast, the EGC region had higher chlorophyll *a* concentration and a strong spring bloom. Thus, the demise of the I-group krill in the Central and Northern region might have been related to food availability that was insufficient to meet their energetic requirements. Studies have shown that the metabolic costs of krill maintaining a pelagic lifestyle increase with increasing body size (Kils 1981; Tarling et al. 2000).

Other studies have shown that krill (*Euphausia superba*) may suffer from higher rates of starvation in the open ocean compared to the shelf edge regions where phytoplankton concentrations are typically higher (Fach et al. 2002). The mixing of populations from different water masses could have also influenced the population structure around the East Greenland shelf break, given that the region is comprised of waters, and hence krill, from several areas (Lavender et al. 2000). To some extent, the results may be a consequence of patch dynamics. Evidence to suggest that different patches might have been sampled during the investigation lies in the fact that the Central and Northern populations comprised a large II-group cohort during spring 2002 when the I-group recruiting to it was absent or in low abundance during the previous winter in 2001/02.

5.5.5. Krill size and growth

The modal sizes of each *M. norvegica* and *T. longicaudata* cohort in the Irminger Sea were compared to the hypothetical growth curves of Einarsson (1945), which are based on the mean length of individuals from various regions around the North Atlantic during spring and summer. Considering that Einarsson's (1945) curves may include a degree of variance due to averaging results from a number of different regions over several years (1924-1939), the general sizes of *M. norvegica* and *T. longicaudata* in the current investigation were similar to those obtained around 70 years ago. No net haul data on the species were collected during the winter period by Einarsson (1945), and such data are few for the open North Atlantic. The results presented here provide valuable insight into the size structure of *M. norvegica* during the autumn/winter season in this region. Results for *M. norvegica* obtained from the Irminger Sea also coincide reasonably well with data from the Skagerrak and the Kattegat (Boysen and Buchholz 1984), and the size of *T. longicaudata* is similar to that observed throughout the North Atlantic by Lindley (1978).

The rates of growth of *M. norvegica* in each region were generally higher than those reported for the same species in the Mediterranean (Labat and Cuzin-Roudy 1999) and higher than those determined for *Euphausia superba* (see review by Nicol, 2000). The growth rates were also greater than the highest values given by Boysen &

Buchholz (1984) for populations in the Kattegat. Problems with estimating krill growth rates by analysis of sequential length-frequency plots from samples collected in open and dynamic systems have been reviewed by Nicol (2000), and these problems should be considered when comparing results from different investigations. The results show that all *M. norvegica* cohorts regressed in size between winter 2001 and spring 2002. This may have been the result of two effects: (i) decrease in the size of individuals over time, and (ii) proportionally greater mortality in the largest individuals. Size reduction ("shrinking") has been observed directly in several species of euphausiids, including *M. norvegica*, and it has been suggested that such behaviour could be an energetic response to fluctuating food supplies (Nicol 2000). Krill in this investigation reduced in size during the period when chlorophyll *a* concentrations (a proxy for food availability) were low (Sanders et al. 2005), between winter and the start of the main spring phytoplankton bloom. A reduction in the size of adult krill in the EGC region was also observed between summer 2002 and winter 2002, indicating that somatic growth of the adults had ended by late summer. Post-bloom conditions were apparent during this time and chlorophyll *a* concentrations were comparatively low in the region. Growth of the juveniles, however, continued during this period. A similar cessation in growth of adults in late summer has been noted in other waters (Cuzin-Roudy et al. 2004).

Regional variability in growth of *M. norvegica* and *T. longicaudata* was low throughout the Irminger Sea, and there were no significant links between growth and the prevailing environmental conditions for these species. This is most likely a function of the high temporal and spatial variability associated with both the biological and physical data. There are, however, a number of other potential environmental factors and complex biological interactions that may drive euphausiid growth in the North Atlantic that were not explored in this investigation. For example, Falk-Petersen & Hopkins (1981) and Cuzin-Roudy et al. (2004) noted that successive changes in phytoplankton composition appeared to be a dominant factor regulating both growth and spawning of these euphausiid species in fjordic systems. These studies suggest that food quality, such as the replacement of diatoms by dinoflagellates, in the euphausiid diet during the productive season, as well as food quantity, plays a crucial part in controlling the physiological functions involved in somatic and reproductive development. Therefore, food quality may alter growth and

reproductive processes, and affect mortality of large adult krill (e.g. II-group), which have higher metabolic demands. Many northern euphausiids also feed upon copepods and other small zooplankton, so chlorophyll *a* concentration alone is not a true indicator of the euphausiid feeding environment. In order to explore regional variability in growth and possible links to the prevailing environmental conditions further, more biological and physical data need to be collected at finer temporal and spatial resolutions. Size-fractionated chlorophyll data and mesozooplankton samples were collected during each of the Marine Productivity research cruises, and it is envisaged that on going analyses will provide further data for such investigations.

5.5.6. Sexual maturity status

Mauchline (1980a) pointed out that maturation and growth of euphausiids are influenced by temperature and food availability in a complex manner, and that breeding patterns may also vary between successive years. Results from this investigation are in accord with Mauchline (1980a), and there is evidence for regional and inter-annual differences in the rate of maturation of *M. norvegica*. Stocks during the spring reproductive season in the Central region of the Irminger Sea were comprised of proportionally more sub-adult krill and fewer females with spermatophores than were stocks in the Northern region or the East Greenland Coast region. Oceanographic data from Holliday et al. (2006) show generally that the Central region had the lowest temperatures in the spring and winter, and that it had only a minor spring phytoplankton bloom. These factors may have significantly reduced the rate of sexual development of the 0-group in the region. Evidence suggesting that the rate of sexual maturation of *M. norvegica* varied inter-annually lies in the fact that post-larvae from the spawning of spring 2001 had reached a more advanced state of sexual maturity by winter than those spawned in spring 2002. All krill had advanced from the juvenile stages to sub-adults by winter 2001/02, but there were a significant proportion of juveniles present in winter 2002/03.

5.5.7. Insight into possible "regime shift"

The North Atlantic is subject to decadal-scale climatic variations, including the North Atlantic Oscillation, which can have significant impacts on the distribution and life cycles of ecologically important zooplankton species in systems that are exploited commercially (Beaugrand 2003; Beaugrand et al. 2002). Furthermore, there is increasing evidence that the impact of such climate-mediated biogeographical shifts in plankton could propagate up pelagic food webs because of tight trophic coupling (Richardson and Schoeman 2004). An original object of our investigation was insight about possible impacts of decadal-scale climate variation on the euphausiid component of the Irminger Sea ecosystem by comparing our findings to existing historic data. Such data include those of Einarsson (1945), that were collected mainly around 1933, and those collected as part of the broad-scale NORWESTLANT programme in 1963 (Anon. 1968). Both these data sets were collected at times when the NAO was in an opposite phase ("low") to that apparent during our investigation ("high"), providing an ostensible means for comparing the distribution and population dynamics of euphausiids at times of contrasting NAO status. However, recent studies have highlighted that substantial time-series data (of at least 28 years) are required to show significant links between changes in zooplankton abundance in a particular region and an indicator of climate change (Planque and Reid 1997). There is also some evidence to suggest that the relationship between population fluctuations in the North Atlantic and the NAO index might be ephemeral, further highlighting the need for data collected at a high temporal resolution (Joyce 2002). In light of this, existing data series from the Irminger Sea are too short to provide meaningful insight into the possible impacts of long-term, broad-scale climate variation on euphausiid distribution and life cycles. Furthermore, examination of the NORWESTLANT survey data shows that the data are largely semi-quantitative and incompatible with the data of this investigation. For example, euphausiids were collected by several research ships, each with different sampling gear and different data recording protocols. No length-frequency data were obtained from the surveys and the volumes filtered by each net were not always recorded. The net hauls were also restricted mainly to the surface layers (upper 50 m) mainly during the daytime, and any semi-quantitative estimates of euphausiid abundance were subject to bias due to diurnal

vertical migration. There is clearly a need for continued investigation and monitoring of key zooplankters in the Irminger Sea and throughout the North Atlantic. We assert that our data provide a benchmark for future investigations into the possible impacts of climate-mediated variation on euphausiids in the Irminger Sea.

5.6. Conclusions

The Irminger Sea is a highly variable system, both temporally and spatially. Our results show a high degree of spatial heterogeneity in the seasonal distribution of euphausiid abundance and biomass, and in the distribution of euphausiid larvae during 2001-2002. There was evidence to suggest regional variability in growth and population dynamics of the two dominant euphausiid species within the Irminger Sea, and this corresponded broadly with distinct physical zones in the basin. There were, however, no significant links between euphausiid growth and temperature or chlorophyll *a* concentration. This was most likely a function of the high temporal and spatial variability inherent in the biological and physical sampling. The data presented in this investigation comprise the first quantitative, broad-scale observations of euphausiids in the Irminger Sea since the 1930s. These data are pre-requisite for understanding ecosystem dynamics in the North Atlantic and for the implementation of robust ecosystem-based management strategies.

6. General discussion and summary

High latitude pelagic environments are ecologically important and are susceptible to over-exploitation and climate change. However, ecological processes and the possible impacts of these pressures are poorly understood in these regions. Quantifying the distribution of abundance of key zooplankton groups and resolving the mechanisms controlling spatial/temporal heterogeneity of these groups at the most appropriate scales are essential prerequisites for robust ecosystem-based management of high latitude pelagic environments. Euphausiids are an integral part of high latitude marine ecosystems, but our understanding of variation in euphausiid distribution, abundance and population processes on sub-annual time scales has been highly confounded. This is primarily due to logistic and financial constraints that limit the amount of empirical data in these regions. South Georgia and the Irminger Sea are two examples of high latitude regions where there is a paucity of within-year data on euphausiids.

At the outset of my research, few studies had attempted to quantify the timing, magnitude and causal mechanisms of short-term, ecologically significant, intra-annual variability in Antarctic krill abundance at South Georgia. Marked intra-annual variation in krill abundance had been hinted at from the few acoustic observations obtained at the island in the same season, and from studies on predators breeding at South Georgia, but there was insufficient data to resolve variation in krill abundance on sub-annual time scales. This was primarily due limitations with conventional ship-based methods used to obtain “snap shot” data on the South Georgia pelagic environment. Investigating short-term, intra-annual variation in krill abundance at South Georgia was important for at least three reasons, in an ecosystem management context. Firstly, the possible existence of significant within-year or seasonal variations in krill abundance had potentially worrying implications for analyses of ecosystem processes at South Georgia that were based on short-term cruise observations, because the timing of the acoustic survey at the island could have significantly affected the estimate of krill density for a given year. Prior to this investigation, it was not clear whether or not apparent inter-annual variation in krill abundance at South Georgia was simply a temporal alias of shorter-term, intra-annual variability. Secondly, scientists had been unable to describe appropriately functional responses (e.g.

breeding success) of krill predators to varying prey availability due to the mismatch between the time scales of vessel surveys (c. 2 weeks duration) and the breeding season (around 4 to 5 months). Thirdly, the causal mechanisms driving intra- and inter-annual variation in krill abundance were unclear and lack of contemporaneous oceanographic and krill data had prevented hypotheses regarding krill flux and variation in the position of the SACCF relative to South Georgia from being tested empirically. Regarding the North Atlantic aspect of the investigation, data on seasonal variation in euphausiid distribution, abundance and population dynamics in the Irminger Sea were limited at the outset of this investigation. Despite several detailed studies of euphausiids in many regions of the North Atlantic (for example, the CPR surveys), there were no seasonal data from the Irminger Sea prior to this study, and the few historic data existing from this region were predominantly limited by a number of factors. In light of recent concern regarding the potential impacts of global climate change on the North Atlantic ecosystem, there was a fundamental need for quantitative, intra-annual data on euphausiids in the Irminger Sea to provide a benchmark for further investigations into climate-mediated ecosystem change in the North Atlantic. In this dissertation, I have attempted to provide new insight into short-term, intra-annual variation in euphausiid abundance, distribution and population dynamics and the casual mechanisms thereof, in two important high latitude ecosystems.

6.1. Summary of results

In this thesis, I have helped to develop and substantiated a new method for monitoring short-term variation in Antarctic krill abundance in relation to underlying oceanography using moored instrument arrays (Chapter 2). Our research leads the field in the use of moorings to measure abundance of krill at South Georgia, and the methods developed as part of this work have wide applications for other biophysical investigations throughout the Southern Ocean and in other seas. Using two mooring arrays, I have provided new insight into the timing and magnitude of intra-annual variation in Antarctic krill density at South Georgia that has hitherto been unavailable from conventional ship-based approaches, and my results comprise the first empirical with-in year time series of krill density at the island, showing a distinct seasonal

pattern in variation (Chapter 3). The data presented here comprise the first observations of krill density at South Georgia from the winter season. The mooring-derived time-series data are innovative for investigations into the functional responses of upper-trophic-level species to fluctuations in prey abundance at South Georgia, and for continuing investigations into variation in krill density at the island on between-year time scales. Furthermore, analyses of the time-series data have provided the first quantitative framework with which to resolve the possibility of temporal aliasing associated with previous and ongoing ship-based survey estimates of krill density at South Georgia. From this framework, I have attempted to quantify the level of variation that would have to exist for an 'annual' shipboard survey to detect a 'high' or 'low' krill density event against the prevailing intra-annual signal, and shown that the notion of large inter-annual variations in krill density at the island, as suggested from previous ecological studies, holds valid. This research has great value for the krill fishery and other scientific krill surveys in the region, and is therefore important for robust ecosystem-based management strategies at the island. I also attempted in this dissertation to evaluate some of the potential biological and oceanographic mechanisms driving short-term variation in krill abundance at South Georgia, such as seasonal variation in the position of the SACCF and predation (Chapter 4). My analyses constitute a major step forward in our understanding of the coupled biological-physical marine system on sub-annual time scales and this work will form the basis for continuing studies to elucidate the causal mechanisms of inter-annual, and possibly decadal scale, variation in krill density at South Georgia and across the Scotia Sea. I also describe in this thesis the seasonal distribution and abundance of euphausiids in the Irminger Sea, and examine regional variation in growth and population dynamics of two key euphausiid species in the North Atlantic in relation to prevailing oceanography in this dissertation (Chapter 5). My data form the most comprehensive net haul data in the Irminger Sea to date and thus constitute a benchmark for studies investigating food web relationships in the North Atlantic and for further investigations into the possible impacts of long-term, broad-scale environmental change on euphausiids in the Irminger Sea and throughout the North Atlantic. My data are also the first to be obtained from the region during the winter season.

6.2. Controls of zooplankton heterogeneity at high latitudes

A central aim of this dissertation was to provide new insight into the most important physical and biological mechanisms controlling macrozooplankton (and some extent, nekton) spatial heterogeneity in these regions using data on the euphausiid-ocean component of the South Georgia and Irminger Sea ecosystems. Although South Georgia and the Irminger Sea are quite different ecosystems, the two regions sustain high euphausiid biomass, share some common environmental characteristics (e.g. low temperature and high seasonality), and are similar in terms of the scale of oceanographic processes that exert control over euphausiid populations (Chapter 1). Therefore, analyses of these systems might tell us something about the predominant mechanisms controlling the patch dynamics of key macrozooplankton groups in high latitude pelagic environments. In this section, I give examples of such mechanisms and how they may force zooplankton spatial heterogeneity, and discuss what this new study tells us about the most important controls at high latitudes. I also compare and contrast some biological aspects of the main euphausiids in the polar/sub-polar regions and consider the possible impacts of human-mediated change on these species.

6.2.1. Temperature

One of the most important abiotic factors affecting marine zooplankton is temperature (Hirst et al. 2003). Variation in temperature can induce significant changes in zooplankton physiology (e.g. ingestion, respiration and excretion), which has a direct impact on natural rates of growth, development, mortality and recruitment (Buchholz 2003; Quetin et al. 1994; Ross et al. 1988). Thus temperature can be a major control on the spatial distribution and abundance of zooplankton populations. High latitude seas are very oceanographically dynamic, and high spatial and temporal variability in temperature occurs within relatively small-scale (within-basin) systems (Holliday et al. 2006; Thorpe et al. 2002). The horizontal, vertical and seasonal range in temperature throughout high latitude seas is around -1.8°C to 4.0°C, and the habitats of many key zooplankton groups are subjected to this entire temperature range (Huntley and Niiler 1995). Although this range is relatively narrow compared to that

of temperate seas (c. 4.0 to 18°C), such small changes in temperature can have a large impact on many high latitude zooplankton groups, including euphausiids (Hirst et al. 2003).

Ross et al. (1988) investigated the effect of temperature on development times and survival of early larval stages of *E. superba* in the southwest Atlantic. Their investigation showed that the development time of *E. superba* embryos and larval stages decreased exponentially with increasing temperature, and that significant changes in development time occurred within a very small temperature range (-1°C to 2°C). For example, embryonic duration increased from 4.8 days at 2°C to 8.3 days at –1°C, a doubling for only a 3°C increase in temperature. These findings were supported by Huntley and Brinton (1991), who showed that larval stages of *E. superba* developed two to three times more rapidly in the Gerlache Strait during localized heating events than did there counterparts in the colder waters of the Bransfield Strait. This study highlights well the importance of temperature in controlling euphausiid distribution and abundance. Ross et al. (1988) further identified another effect of temperature. These authors showed that early larval stages of *E. superba* have a cold sensitive period during their lifecycle that is independent of food availability. Larval stages reared at -1°C died within 3 days of metamorphosis to Calyptopis 1, while siblings at higher temperatures developed normally and survived. The physiological mechanisms behind this temperature sensitivity are unknown, but the authors suggested that changes in proteins associated with regulatory functions or decreased protein synthesis might be important. A cold sensitive period during the early life stages of *E. superba* has important ecological implications. If populations of adult krill spawn in areas where embryos or larvae will encounter -1°C during the temperature sensitive period, the larvae will not survive and recruitment in these waters will be low. Conversely, if embryos are released in waters where they are not exposed to subzero temperatures during a temperature sensitive period, recruitment will be higher. Few studies have focused on the effect of temperature on the larvae of northern euphausiids, but the available data suggest that the development and survival of *M. norvegica* and *Thysanoessa* larvae is also controlled in similar way to that of *E. superba* (Mauchline 1977). However, spawning of *M. norvegica* is confined to waters >5°C and most *Thysanoessa* species spawn outside of the cold Arctic waters

(Astthorsson and Gislason 1997; Dalpadado and Skjoldal 1996), indicating the dominant northern species are less cold-tolerant than *E. superba*.

Experimental and field studies have revealed how environmental variability affects the physiology of adult and post-larvae euphausiids (Buchholz 2003; Nicol 2000; Quetin et al. 1994). The general pattern for euphausiids and many other marine zooplankton groups is that, within a species-specific temperature range, low water temperatures incur slow metabolic rates, reduced rates of growth, lower rates of reproduction and longer lifecycles compared to warm temperatures (Hirst et al. 2003). Many high latitude organisms are stenothermal and variations in temperature beyond their functional range can have a negative impact on populations (Peck et al. 2004). *E. superba* is confined to polar waters and is an good example of a stenothermic organism (Buchholz and Saborowski 2000). The impact of environmental variation on natural growth rates in *E. superba* was investigated by Atkinson et al. (2006). These authors observed a marked decline in daily growth rate of *E. superba* at higher temperatures within the southwest Atlantic. Specifically, krill at South Georgia had slower growth rates in summer than krill in regions further south where the water was colder. Prior to the study it was generally assumed that krill growth was maximal at South Georgia due to the warm water and plentiful food in summer (Atkinson et al. 2001; Reid et al. 2002). The temperature range of the study was 5°C, almost the species entire range (Quetin et al. 1994). Other Antarctic species suffer a 50% loss of activity at 2-3°C and complete losses at 5°C, which reflects rapid increases in respiration cost with temperature and the onset of anaerobic metabolism (Peck et al. 2004). Atkinson et al. (2006) therefore suggested that the slow growth rates at the northern limit of *E. superba's* distributional range reflected the onset of thermal stress, and that South Georgia might have become thermally suboptimal for krill in the summer. The narrow temperature range of *E. superba* contrasts markedly with that of northern species, particularly *M. norvegica*. Studies have shown that *M. norvegica* has a high level of physiological plasticity and that populations are adapted to very different environmental conditions (Buchholz and Saborowski 2000; Saborowski et al. 2002; Virtue et al. 2000). For example, the species occurs in diverse environments along European coasts and adjacent seas, from the shallow, cold (5-10°C) Clyde Sea area (western Scotland), Kattegat (east Denmark) and Skagerrak (west Sweden), to the deep and constantly warm (c. 13°C) and oligotrophic Ligurian Sea (northwest

Mediterranean). Thus *M. norvegica* has the capacity to physiologically cope with a wide range of temperature regimes and the species is not stenothermal.

6.2.2. Sea-ice

The presence of sea-ice has an important role in high latitude ecosystem function as it provides a unique habitat for many zooplankton species, and the life-cycles of many zooplankton groups are tightly coupled with seasonal sea-ice dynamics (Voronina et al. 2001). For example, the sea-ice habitat is particularly considered important for Southern Ocean euphausiids. Studies in the South Atlantic suggest that regional krill abundance is positively related to the extent of sea-ice the previous winter (Brierley and Watkins 2000; Hewitt et al. 2003), and that historically there is a relationship between the extent of winter sea-ice and the overall krill abundance in the South Atlantic (Atkinson et al. 2004). The mechanism proposed for such a relationship is that the community of microorganisms growing on the underside of the ice provides food for overwintering adult and larval krill (and other zooplankton), and this under-ice community seeds the surface waters with algae in spring when the ice melts. Thus, larger extents of sea-ice result in more extensive sea-ice communities and, consequently, in more favourable grazing conditions both in winter and spring, when more algal biomass is released into the surface waters (Daly 1990; Leob et al. 1997; Marschall 1988; Nicol 2006; Smetacek et al. 1990). However, the relationship between sea-ice extent and the biomass of the ice community has not yet been verified empirically (Brierley and Thomas 2002). It has also been suggest that pelagic organisms employ the sea-ice as a refuge from predation (Marschall 1988; Quetin and Ross 2001; Siegel and Leob 1995).

Although sea-ice has been identified as being important in the lifecycle of *E. superba* and some other Southern Ocean euphausiids (Nicol 2006), the importance of sea-ice to the lifecycles of euphausiids in the northern hemisphere is not strictly clear. It has been assumed widely from Southern Ocean studies that sea-ice plays a similar functional role for northern species as it does for southern species, but there is paucity of data on northern euphausiids and sea-ice dynamics. Studies suggest that the ecology of *M. norvegia* and *T. longicaudata* might not be as tightly coupled with sea-

ice as that of *E. superba* (for example, *M. norvegia* populations attain high abundance in a range of ice-free environments and the main centre of distribution of *T. longicaudata* occurs away from the sea-ice sectors; Lindley 1978; Seigel 2000a), but variations in sea-ice could still lead to a significant impact on the abundance of euphausiids in certain regions. In light of recent studies showing a marked decline in sea-ice cover in the Arctic regions (Overpeck et al. 2005; Rothrock et al. 1999), there is a pressing need to understand the role of sea-ice in the lifecycles of northern euphausiid species in the sea-ice sectors. Likewise, further studies are required in the Southern Ocean. There is now increasing evidence that the climate at the Antarctic Peninsula has been warming faster than any other part of the planent and marked reductions in winter sea-ice cover have been observed (Curran et al. 2003; De La Mare 1997; Moline et al. 2004). This region is considered cruicial for the recruitment of *E. superba* in the southwestern Atlantic. As the species has a lifecycle that is potentially highly dependent on the sea-ice environment, large-scale reductions in sea-ice cover could have a detrimental impact on krill abundance in the region, with large implications for the Southern Ocean ecosystem.

6.2.3. Food availability

The development and growth of individual zooplankton, and the survival of zooplankton populations, is critically dependent on the availability of food resources and temperature (Hirst et al. 2003). Without adequate food supplies, development and growth can be reduced, reproductive capacity curtailed and mortality increased (Ross and Quetin 1989; Ross et al. 2000). Thus high spatial variability in food availability may lead to high spatial heterogeneity in zooplankton distribution, abundance and population dynamics. Autotrophic organisms form the base of pelagic food webs and food availability for zooplankton is related largely to primary productivity. Primary production is highly variable in space and time at high latitudes, and the controls of such variation may be complex (Sakshaug 1997). However, some generalizations on the temporal and regional availability of food resources can be made. Throughout high latitude seas, primary productivity is greatest in spring and summer, and diminishes to negligible amounts during the winter. Although some primary production occurs within annual sea-ice in the winter season, it makes a relatively

minor contribution to the total annual primary production (Huntley and Niiler 1995). Regionally, the greatest standing stocks of primary production generally occur in coastal and on-shelf locations, along shelf breaks and around oceanic ridges, although high productivity can also occur around frontal zones and eddie formations (Lalli and Parsons 1997). These regions may therefore sustain higher secondary production and better feeding environments than open oceanic regions where food availability is comparably lower.

As well as abundance of food resources in the pelagic environment, the feeding ecology of zooplankton is an important factor in determining spatial heterogeneity. High latitude euphausiids, for example, have various feeding regimes (e.g. herbivourous or omnivorous) and utilize food resources differently depending on their lifecycle stratergy and ecological niche (Falk-Petersen et al. 2000). Ross et al. (1988) also suggested that euphausiids might utilize different food types at different stages of development, and showed that correct food type was particularly important for the survival of early euphausiid larval stages (Calytopis 1). Thus food quality has a cruicial role in controlling euphausiid populations (Cuzin-Roudy et al. 2004). There is a notable difference between the Irminger Sea and the Southern Ocean in terms of the feeding ecology of the dominant euphausiid species. Studies have shown that *M. norvegica* and *T. longicaudata* in the North Atlantic and Arctic waters are omnivorous but largely carnivorous, feeding mainly on calanoid copepods and other small zooplankton (Bamstedt and Karlson 1998; Falk-Petersen et al. 2000; Virtue et al. 2000). Phytoplankton lipid contributes only a small proportion to the diet of these species in these regions. Indeed, McClatchie (1985) indicated that *M. norvegica* cannot survive on a pure phytoplankton diet in these regions, but needs large copepods in high abundance (>19 copepods l^{-1}) to meet its metabolic demands of 4.6% of krill body energy d^{-1}. *E. superba* is also considered to be omnivorous, but in contrast to the two northern species, it has a large dietary input of phytoplankton and feeds less intensively on copepods (Falk-Petersen et al. 2000; Schmidt et al. 2006). However, the species has a flexible diet and may consume large proportions of copepods in some situations (Atkinson et al. 1999). A further difference is that *E. superba* shows less pronounced lipid storage than *M. norvegia* and *T. longicaudata* (Falk-Petersen et al. 2000). As well as lipid stores, *E. superba* relies heavily on detritus and ice algae for overwinter survival, and are highly dependent on dietary

input from the spring bloom to reproduce as gonad maturation and egg production are not fuelled by lipid reserves during the winter period (Cuzin-Roudy 2000; Falk-Petersen et al. 2000). In contrast, *M. norvegica* and *T. longicaudata* build up high lipid reserves that may be sufficient to fuel initial reproductive development and help sustain metabolic demands during the winter (Mauchline 1980a).

To some extent, euphausiid feeding ecology and regional variation in primary production may explain the distribution of the main euphausiids in the two systems studied in this thesis. For example, *E. superba* feeds largely on phytoplankton and occurs in greatest abundance in regions of elevated primary productivity (including under sea-ice) (Brierley et al. 2002a; Nicol 2006). The species does not inhabit regions with low productivity, such as the SACCF, where phytoplankton concentrations are markedly low (Hofmann and Murphy 2004). Greatest abundance of *M. norvegica* and *T. longicaudata* also occurs generally in regions of high primary production (and hence, secondary production) in the North Atlantic (Saunders et al. 2007). However, studies have shown that these species, particularly *M. norvegica*, can survive in high abundance in oligotrophic regions, suggesting that the situation is more complex and other factors are involved (Buchholz and Saborowski 2000; Cuzin-Roudy and Buchholz 1999; Labat and Cuzin-Roudy 1999).

6.2.4. Horizontal advection

Huntley and Niiler (1995) assert that horizontal advection is the single most important physical mechanism controlling zooplankton spatial heterogeneity in high latitude seas, and that the physical processes in these regions are different from those in all other oceans. For example, advection determines whether or not zooplankton (and to some extent, nekton) will reside in food-rich (e.g. shelf-break regions) or food-poor regions, and the morphology of the advective features further determines the residence time in a given food or temperature regime. Thus advection has a direct impact on rates of growth, mortality, reproduction, and ultimately, the distribution of zooplankton abundance. Advective processes (e.g. baroclinic eddies and frontal zones) at high latitudes are different to those at lower latitudes primarily due to differences in their natural horizontal scales. The spatial scale of circulation

(determined by the internal Rossby radius) is dramatically altered with latitude, and advective forces at high latitudes operate at much smaller scales (order 10 km) to those at lower latitudes (order >100 km in the subtropics) (Huntley and Niiler 1995). Consequently, the intensity of advection on such small scales causes zooplankton populations to be more highly dispersed in high latitude systems.

6.2.5. Impact of climate change on high latitude euphausiids

The ecology of the main euphausiids of the North and South Atlantic is different in many resects and the species' may respond differently to a warming global climate. The species that appears most at threat from long-term climate change is *E. superba*. *E. superba* is confined to the cold polar waters. The species has a stenothermal physiology and its lifecycle depends highly on the sea-ice environment. Although *E. superba* can adapt to different feeding environments, the species appears not to have the capacity to adapt to increasing temperatures (Buchholz and Saborowski 2000). Sea temperatures have risen by ~1°C since 1925-1939 and are likely to continue to increase over the next 50 years (Whitehouse et al. 1996). This may have a large impact on krill abundance in the Southern Ocean, particularly at South Georgia where there is evidence to suggest that the species is susceptible to thermal stress (Atkinson et al. 2006). Furthermore, a decrease in winter sea-extent and duration is expected at the Antarctic Peninsula, a region considered crucial for krill recruitment and over-winter survival in the southwestern Atlantic sector of the Southern Ocean (Overpeck et al. 2005; Rothrock et al. 1999). This may also lead to major reductions in krill abundance, with potentially worrying ecological consequences across the Scotia Sea. In contrast, *M. norvegica* and *T. longicaudata* in the Northern Hemisphere appear to be less susceptible to a warming climate. These boreal species have the capacity to adapt to different feeding environments and are able to function at higher temperature ranges. The lifecycles of *M. norvegica* and *T. longicaudata* also seem less coupled with the sea-ice environment. However, there could be a combination of other factors controlling high latitude euphausiids. The potential impacts of climate change are likely to be complex and it is not clear how euphausiids in either hemisphere will react to such long-term forcing. Thus further investigations are necessary to aid effective ecosystem management in high latitude regions.

6.2.6. New insight

In order to gain new insight into the physical controls that force zooplankton heterogeneity at high latitudes, it is first necessary to resolve sufficiently the spatial and temporal variability of such phenomena and their interaction with the temporal and spatial variability that characterizes zooplankton populations (Huntley and Niiler 1995). Although the North Atlantic aspect of this investigation provides valuable new information on the intra-annual variability of zooplankton distribution, abundance and population processes in an important high latitude ecosystem, unequivocal links between biological variation and the observed physical variation were generally not sufficient to make any solid inferences on the most important physical controls. For example, a high degree of spatial heterogeneity in the seasonal distribution of euphausiid abundance/biomass was detected in the Irminger Sea during 2001 2002, and there was some evidence of regional differences in population structure of the two dominant euphausiid species (Chapter 5). Although some of this variability coincided broadly with distinct physical zones in the Irminger Sea, links between biological and physical interactions were tentative and it can only be concluded that food availability, temperature, animal behaviour, advective processes and sea-ice are likely to be important factors. The study highlights the problem of temporal and spatial variability in resolving physical forcing on zooplankton populations in high latitude ecosystems.

The South Atlantic aspect of this dissertation presents similar problems in establishing the most important controls on zooplankton spatial heterogeneity at high latitudes. A distinct and repeatable pattern of seasonal variation in euphausiid abundance was detected at South Georgia by on-shelf and off-shelf moorings (Chapters 4 and 3). This seasonal pattern of variation was significantly correlated with seasonal variation in temperature at the island, suggesting that temperature might be an important control. However, correlation does not prove cause and effect, and it is possible that other factors were involved (Brierley et al. 1999b). In general, the data were consistent with the notion of large seasonal krill fluxes at the island, and of a predator driven reduction in krill abundance (Chapter 4). Thus, it can be inferred that advection and predation might be the most important controls on macrozooplankton spatial heterogeneity. However, it is difficult to substantiate the impact of horizontal

advection on euphausiid abundance at South Georgia using just data from this investigation. The exact physical processes controlling variability in krill abundance at South Georgia, such as the SACCF, remain largely unresolved, and therefore, it is not possible to discount other controlling mechanisms. Furthermore, the data represent point observations in an ecosystem characterized by high spatial and temporal variability, and it is necessary to understand biological and physical variability on wider spatial scales. There could be various mechanisms operating within the Scotia Sea that affect krill abundance at South Georgia. From this investigation, it is evident that new insights into the controls on marcozooplankon spatial heterogeneity at high latitudes as a whole, are difficult to obtain within relatively small systems such as the Irminger and South Georgia. Further data are clearly needed before any robust inferences can be made on the important physical and biological controls at South Georgia, in the Irminger Sea and ultimately in high latitude ecosystems.

A further consideration is that the coherence of a zooplankton population in space is influenced not only by physical processes, but also animal behaviour (Huntley and Niiler 1995; Nicol 2006). Although zooplankton are often considered as passive drifters in the flow field, many groups are capable of active vertical or horizontal movement (the extent of which is governed by size) and this independent motion can have a significant impact on their distribution (Lalli and Parsons 1997). For example, many zooplankton species perform diel vertical migration (DVM), and studies have shown that animals capable of this behaviour are able to modulate their net horizontal position in the water column by migrating vertically through different motile water masses (Tarling et al. 1998). The formation of swarming and aggregations is another important behavioural mechanism. Studies have shown that some groups, such as euphausiids, form dense swarms or aggregations that are capable of active horizontal movement (Hamner and Hamner 2000). However, the exact external cues controlling such behaviour are not yet known. The impact of such behavioural mechanisms is unknown in this investigation, though it is possible they had a considerable effect. Quantifying the role and causes of zooplankton behaviour in determining spatial heterogeneity is problematical due to sampling limitations. Consequently, many studies have tended to placed more emphasis on physical mechanisms (Nicol 2003). However, behavioural mechanisms clearly warrant detailed investigation and need to

be considered further in order to fully understand temporal and spatial variability in zooplankton abundance at high latitudes (Nicol 2003).

6.3. Possible future work and recommendations

Moorings provide a new window of observation into the coupled biological-physical regime in the pelagic environment, and the systems described in this thesis have wide applications in biological oceanography. In particular, increased use of these platforms, together with conventional ship-based and modelling methods, could provide a wealth of new information on krill ecology throughout the Southern Ocean that may aid ecosystem management. For example, these systems could be used over a wider spatial scale to monitor continuously krill abundance and oceanographic transport mechanisms across the Scotia Sea. Time-series data from several moorings deployed simultaneously around the Antarctic Peninsula, South Orkney Islands, mid-Scotia Sea, South Sandwich Islands and South Georgia, would lead to much improved understanding of krill flux across the Scotia Sea and provide new insight into regional ecosystem function at each location. Data from such arrays would also improve our understanding of diel and seasonal migratory behaviour of krill and other Southern Ocean zooplankton (Enderlein et al. submitted). The current design of the mooring arrays could be improved for furture deployments by the addition of downward-looking sensors. The results presented in this thesis and elsewhere suggest that krill may reside below the depth of our moorings (c. 200 m) in some instances (e.g. during winter). It is therefore possible that important seasonal events are being missed. Downward-looking instruments would resolve this issue by increasing the vertical range for monitoring krill density. As high-frequency acoustic data (120 kHz and above) from shipboard platforms have been restricted largely to the layers above 250 m (due to spherical spreading and attenuation of the transmitted acoustic pulse), such an approach would provide new insight into the ecology of Antarctic krill and other zooplankon.

Application of moorings could provide new insight into the ecology of krill under sea-ice in the Southern Ocean. Although sea-ice has been implicated as a major factor affecting krill abundance, little is known of the way in which ice cover may influence

krill distribution and behaviour, and there are only a few direct observations of krill under ice at the scale necessary for robust density estimation (Brierley et al. 2002a; Brierley and Watkins 2000). Moorings deployed on transects in sea-ice zones (e.g. Antarctic Peninsula, South Orkneys) could be used to gather time-series data on krill abundance under the winter/spring sea-ice. Such data would compliment existing krill studies using autonomous underwater vehicles (AUV). The data might also be useful for investigations into regional changes in krill abundance associated with interannual and longer-term changes in the extent of sea-ice cover

A further application of the moorings is that they can be used to characterize krill aggregation morphology and provide new insight on krill swarming behaviour in the Southern Ocean in relation to physical oceanography. The use of school detection algorithms has produced a wealth of information on aggregation morphology, distribution and density of many acoustically-detected pelagic species, including Antarctic krill (Demer et al. 2000; Hamner and Hamner 2000; Miller and Hampton 1989; Woodd-Walker et al. 2003), and there is some evidence to suggest that krill swarm size may vary with regional krill density (Watkins et al. 1999a). However, there is a paucity of time-series data on krill aggregations. Analyses of mooring data will lead to greater understanding of krill swarm dynamics and enable scientists to establish whether or not krill swarms size varies with regional density at an appropriate temporal resolution. Such analyses are currently ongoing using both mooring data and ship data obtained during the time-series described in this thesis.

6.4. Conclusions

In conclusion, high latitude ecosystems are characterized by spatial and temporal variability. The work presented in this investigation demonstrate that the coupled biophysical regime in high latitude marine ecosystems may be complex as a consequence of such variation, and that it may be difficult to establish robust links between variability in zooplankton distribution/abundance and any singular oceanographic or biological forcing mechanism in these regions. The work presented in this thesis increases our understanding of two important high latitude ecosystems, but further investigations are required in order to resolve the causal mechanisms of

zooplankton spatial heterogeneity in high latitude regions as a whole. The thesis also demonstrates that in order to quantify spatial heterogeneity, and the causal mechanism thereof, small-scale, short-term biological data are essential. Such data are required for making inferences on spatial heterogeneity on broader temporal and spatial scales.

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8. Appendix

In this section is a copy of a publication of which I am first author:

SAUNDERS, R. A., A. INGVARSDOTTIR, J. RASMUSSEN, S. J. HAY, and A. S. BRIERLEY. 2007. Regional variation in distribution pattern, population structure and growth rates of *Meganyctiphanes norvegica* and *Thysanoessa longicaudata* in the Irminger Sea, North Atlantic. Progress in Oceanography **72:** 313-342.